

**SOME ASPECTS OF THE CARRYING CAPACITY
OF PRINCE WILLIAM SOUND, ALASKA
FOR HATCHERY RELEASED PINK AND CHUM SALMON FRY**

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Graduate assistant Dave Urquhart
samples pink salmon fry in Sawmill
Bay, Prince William Sound, Alaska.

Photo by John Hilsinger.

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ABSTRACT

Studies designed to evaluate the impact of localized releases of hatchery reared fry on adjacent estuarine waters are described. At the Evan's Island (Port San Juan) facility, operated by the Prince William Sound Aquaculture Corporation, most hatchery fry moved rapidly away from the immediate area of the site after release, eventually schooling around the shores of several small islands in nearby Elrington Passage. Here the fry remained for several weeks, feeding and growing close to the rocky beaches on an apparently abundant planktonic food supply. By early summer these same fishes had grown to approximately 60 mm in length and began moving offshore and southward from the islands. This change in behavior is probably related to a need for larger food items which cannot be obtained in shallow water, coupled with physiological changes related to the smolting phenomena. We could find no evidence that overcrowding was occurring at locations designated by us as nursery areas. Although the standing stock of potential food at any particular time was never unusually high, the daily tides in this area presented a flux of particles which seemed entirely adequate.

Predation on newly released fry was clearly a problem next to the hatchery. Here, large schools of adult tomcod consistently patrolled the shore and dock areas taking fry when they could. These predators were particularly evident in late April during the peak in outmigration. Later in May, when many fry were held in large saltwater pens for experimental feeding studies, tomcod were still observed in abundance. Upon our recommendation, the holding pens were towed away from the site for release of the fry close to the feeding areas.

An evaluation of the biological oceanography of Prince William Sound is discussed as it applies to hatchery rearing of salmonids in general.

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INTRODUCTION AND STUDY GOALS

In November 1975, the University of Alaska, Institute of Marine Science, with support from the Alaska Sea Grant Program initiated studies of the carrying capacity of estuarine waters adjacent to a developing non-profit salmon hatchery at Port San Juan, Evans Island, Prince William Sound, Alaska (see Appendix I). Scheduled to incubate 20 million pink and chum salmon eggs by 1977, the Prince William Sound Aquaculture Corporation (PWSAC) requested assistance from the University to evaluate the productivity of the waters near the hatchery that would receive large numbers of introduced fry.

The University responded with a small field program in the spring of 1976 designed to detail aspects of the oceanography at the site, and to describe the feeding behavior of fry released from the hatchery. Difficulties with the freshwater supply to the hatchery during the previous winter caused a major change of plans at the site. The eggs were replanted in nearby Larson Creek and subsequently the fry emerged from this stream rather than from the hatchery as planned. Using a small boat and taking advantage of breaks in the weather, the field party collected oceanographic information and samples of fry from April through mid-June. The major effort this first year was directed toward understanding the hydrography, animal plankton standing stock and species succession in Sawmill Bay and nearby Elrington and Latouche Passages.

The winter of 1976-77 was unusually mild in southwestern Alaska; salmon began moving into the estuary in early February. The University responded with a second field party in late March and early April. Since the hatchery was incubating approximately 10 million eggs, we expected large numbers of fry in Sawmill Bay and adjacent waters.

Our goals for this past season were to carefully describe the feeding dependencies of the fry inasmuch as they could be followed through both time and space. The literature suggests that "first feeding" fry may be linked by food abundance to shallow water benthic detrital systems. If this was indeed the case at Sawmill Bay, carrying capacity could become very site specific and perhaps limiting to survival, with high numbers of fry competing for food in spatially restricted seabed feeding regimes. In the spring of 1977, the field work emphasized following and collecting the fry and their food. This time the release was from the hatchery as scheduled and carefully documented from week to week. Our field operation was closed in early July when the fishes become too active for routine sampling. During this last summer, approximately 12,000 fry were collected for growth and feeding studies at 31 locations; 134 zooplankton samples were also obtained at 34 sites. In addition, five experiments were conducted involving fry growth and survival in saltwater pens. While many of these collections remain only partially analysed, a considerable amount of preliminary information is available now for a first-order synthesis. This report represents the synthesis.

RESULTS

In 1976, fry began moving into Sawmill Bay about mid-May. At this time, zooplankton retained by nets of 0.216 mm mesh size (potential fry food) were observed declining in the upper 20 m at Station 2 in Sawmill Bay from a high of over 1000 individuals per m^3 in late April to fewer than 100 per m^3 a month later (Figs. 1, 2). As the fry outmigration proceeded into June, the zooplankton community increased again in abundance (Fig. 3). This relationship was observed again in 1977 but the timing was displaced into late April because of warmer spring temperatures (Fig. 4).

The significance of this phasing cannot be directly ascertained since it is more likely that the flux of food (i.e., movement with the tides) through any particular location is the important factor, rather than the standing stock of plankton at any given location and time. We do know that approximately 58,000 adults returned to Sawmill Bay in the summer of 1977 as spawners which indicates an above average survival over the normal 1 to 2 percent experienced by wild stocks (Bailey, 1969).

Unfortunately, we have no measurements of other food sources which the fry may have used, such as benthic meiofauna, to compare with the timing of the release or the phasing of biological events observed in the water column. We note that a cycling of pelagic food abundance in an amount differing by about a factor of 10 was apparently not detrimental. These observations could be interpreted to mean that critical food levels were never reached even at the lowest levels of animal plankton, or that the pelagic system was not as important as other sources in supporting the first feeding fishes.

As we did not survey areas outside Sawmill Bay in 1976 for fry, we have no idea whether the nursery areas found during the next field season

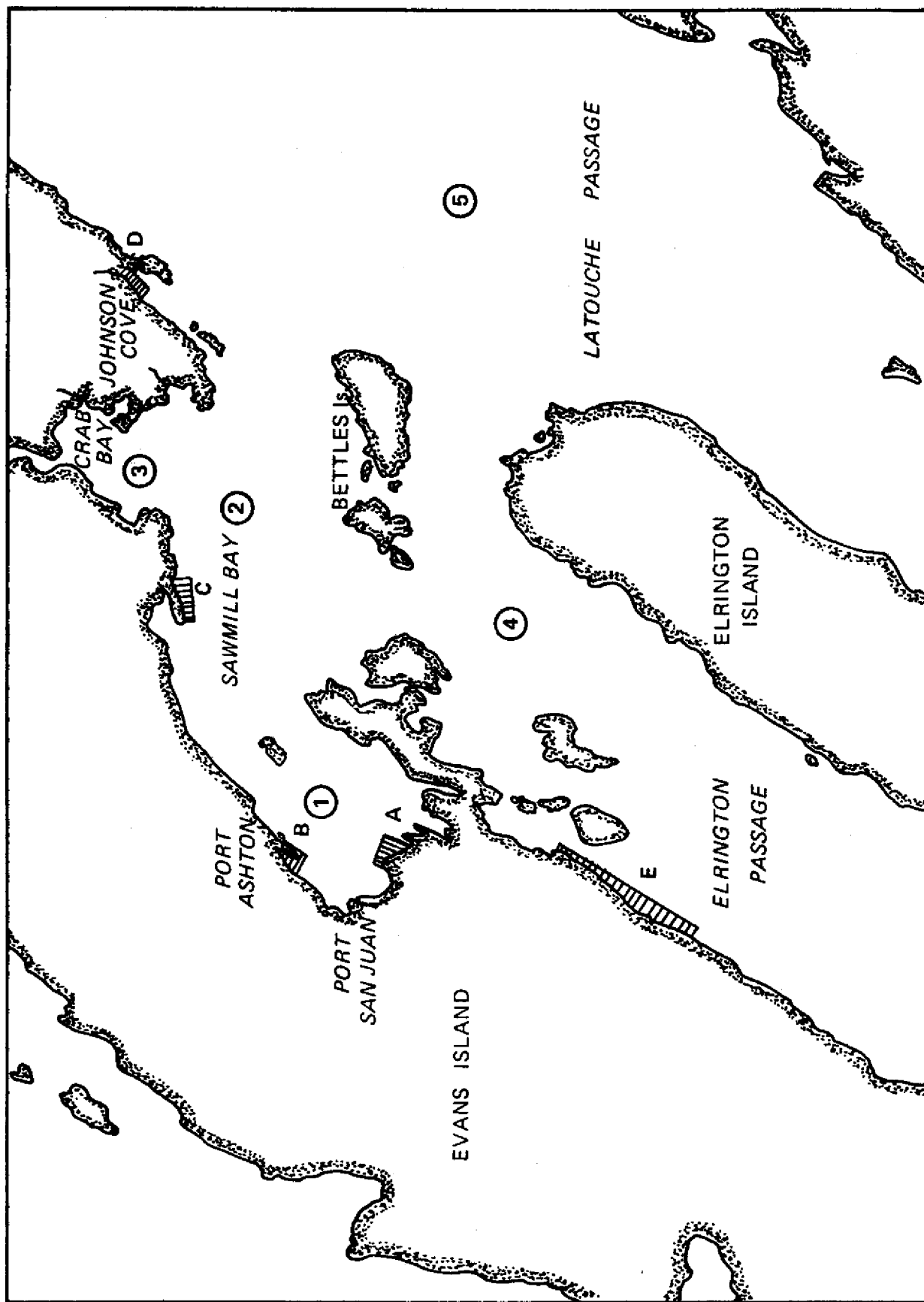


Figure 1. The location of areas examined for fry (hatched) and occupied for oceanographic observations (numbers 1 through 5) in 1976.

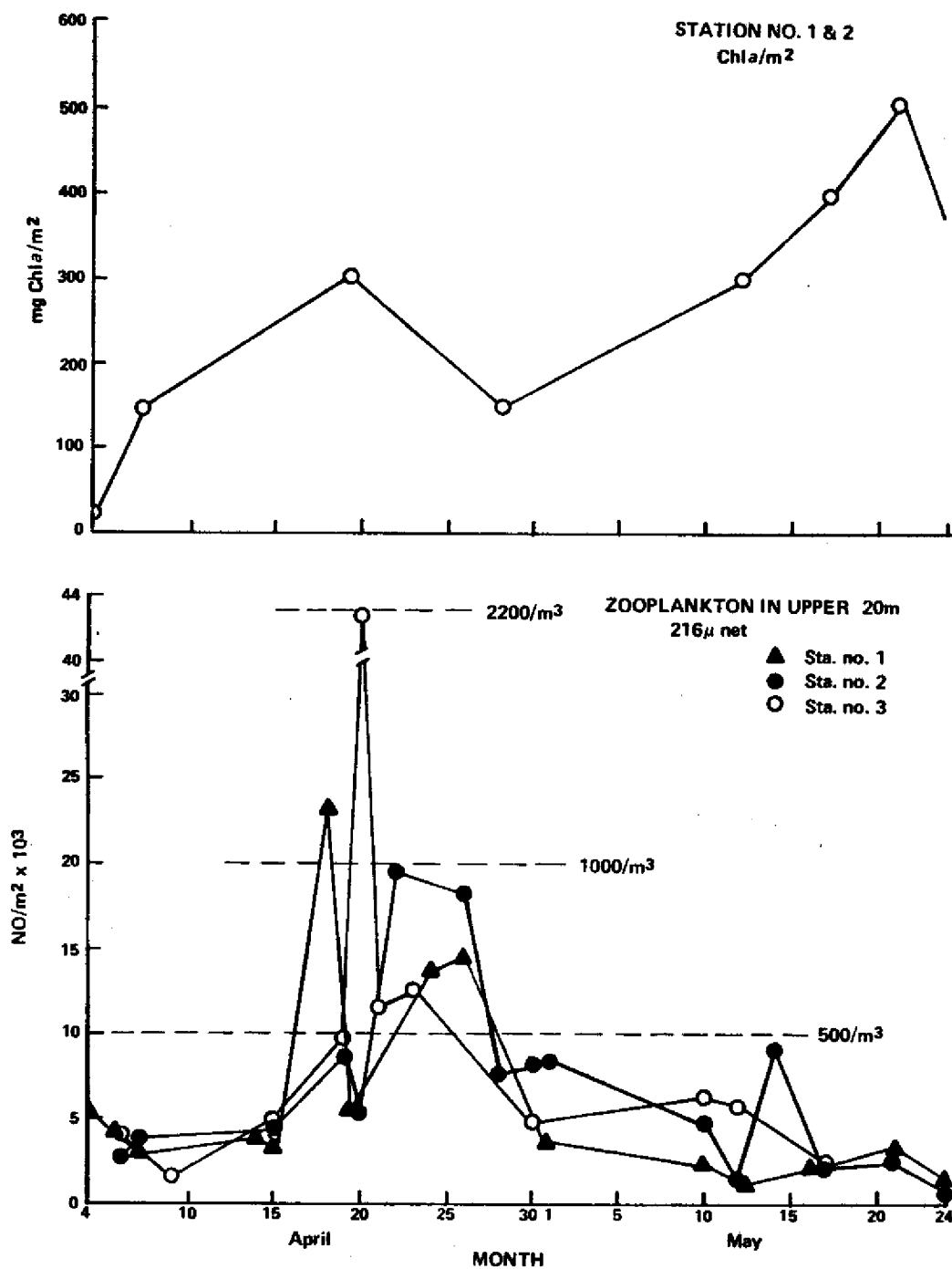


Figure 2. The distribution of chlorophyll and animal plankton at selected oceanographic station, 1976.

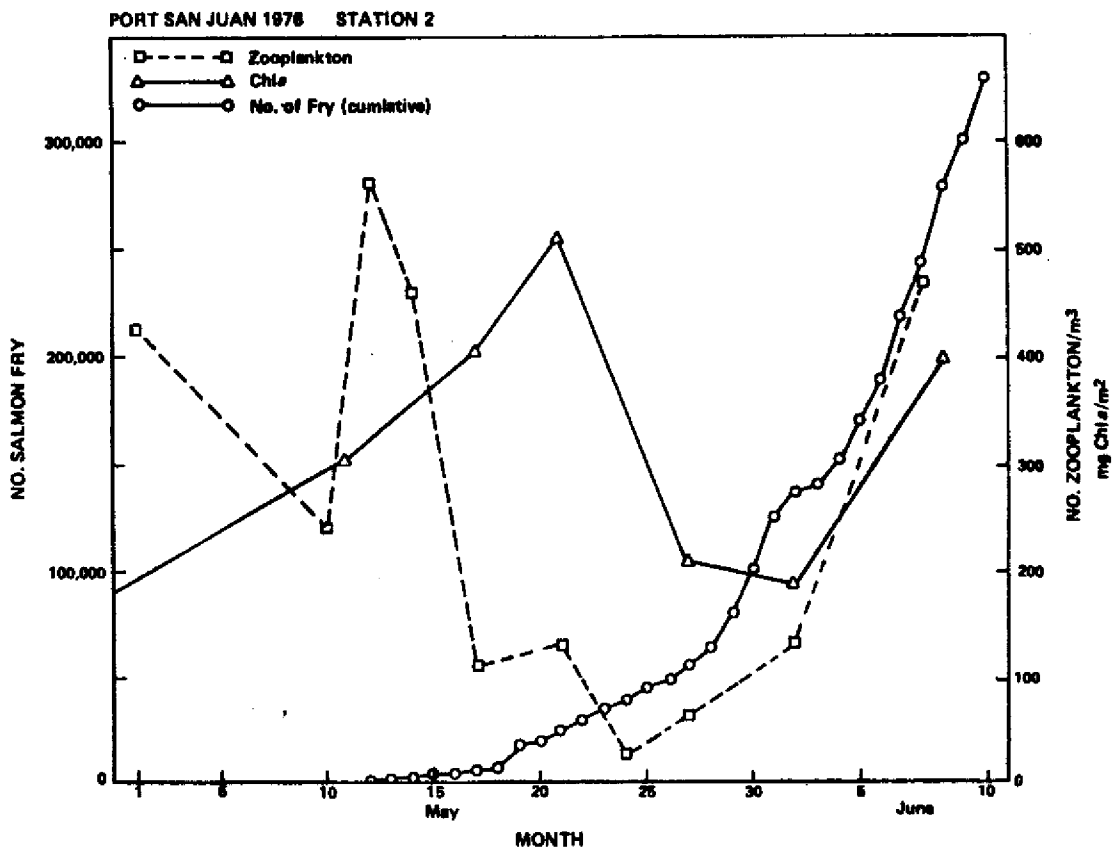


Figure 3. Relationship between chlorophyll, zooplankton, and emerging fry.

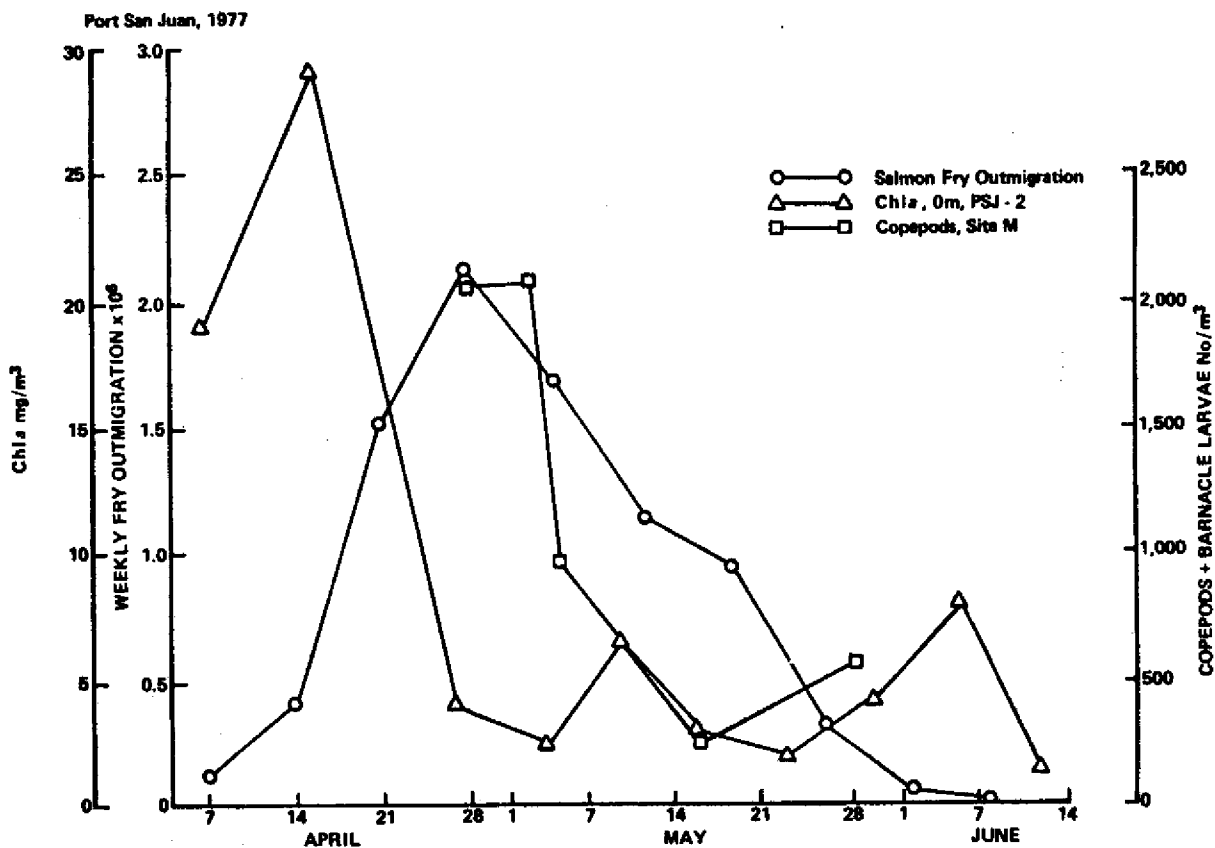


Figure 4. Distributions of chlorophyll, copepods, and emerging salmon; April through June, 1977.

were occupied. Also, our inexperience with small boat operations and fry sampling, particularly beach seining, limited the number of small fishes caught and processed. The few gut analyses we did perform indicated a diet preference for benthic and neritic copepods, and cladocerns usually associated with brackish rather than marine waters. These few observations were used to plan for the next year's field study which included preparations to sample the meiobenthos if necessary, locate the nursery areas, and describe the phasing of biological productivity in the water as it might effect survival in relation to feeding.

Our findings for the 1977 field season can are described in detail as follows:

Fry Incubation and Release

Between August 25 and September 21, 1976, Prince William Sound Aquaculture Corporation received and processed for artificial rearing approximately 14.7 million "green" pink salmon eggs (PWSAC report to ADF&G June, 1977). Five percent of these eggs were taken from Larson Creek adjacent to the Port San Juan hatchery. The rest came from Millard Creek and the Duck River in Galena Bay, northeast Prince William Sound.

Pink salmon eggs generally incubate for 60 to 90 days before hatching (McNeil, 1964). In Alaska, the alevins then spend at least four months developing within the interstices of the streambed gravel before migrating to the sea (Hunter, 1959). Development, and the timing of emergence is primarily determined by stream temperatures (Sheridan, 1962). Pink salmon eggs are known for their ability to tolerate extended periods of very low temperatures, down to 0.5°C, as long as incubation temperatures are above 5.5°C during the first month after deposition (Combs, 1965).

In the Prince William Sound region, stream temperatures normally drop to 1°C during the winter for many weeks (Merrell, 1962).

At Port San Juan, the hatchery water temperatures ranged between 11.5° and 8.5°C while eggs were being processed in late summer. It was not until October 25 that temperatures dropped below the critical 5.5°C level. As previously mentioned, the winter of 1976-1977 was by all accounts extremely mild for all of Alaska. Intake water temperatures for the hatchery averaged above 2°C, with 1.6°C being the lowest value recorded (PWSAC report to ADF&G, June 1977). As a result of the warmer than average water temperatures, fry development took significantly less time and the subsequent outmigration began early. Fry first left the incubation boxes on February 18 with the peak in daily outmigration occurring on April 22 at nearly 450,000 (Fig. 5). The last fry were released on May 29. On the average it took about 230 days for an egg to develop into an emerging pink salmon at Port San Juan during the winter of 1976-1977. The curve representing daily outmigration of fry is shifted to the left by about two weeks due to the warm winter temperatures. By way of comparison, the seasonal timing of emergence for the fry leaving the hatchery at Port San Juan in the spring of 1977 is about what might be expected during a normal year in central British Columbia, 800 km farther south (Hunter, 1969). For purposes of our carrying capacity study, the field party from the University of Alaska's Institute of Marine Science arrived at Port San Juan on April 1 to begin their study of fry feeding and migration behavior. At that time only about 1 percent of the total fry that were to emerge had been released.

Of the "green" eggs that were received and processed by the hatchery in the fall of 1976, 77 percent survived to the "eyed egg" stage; 11.3

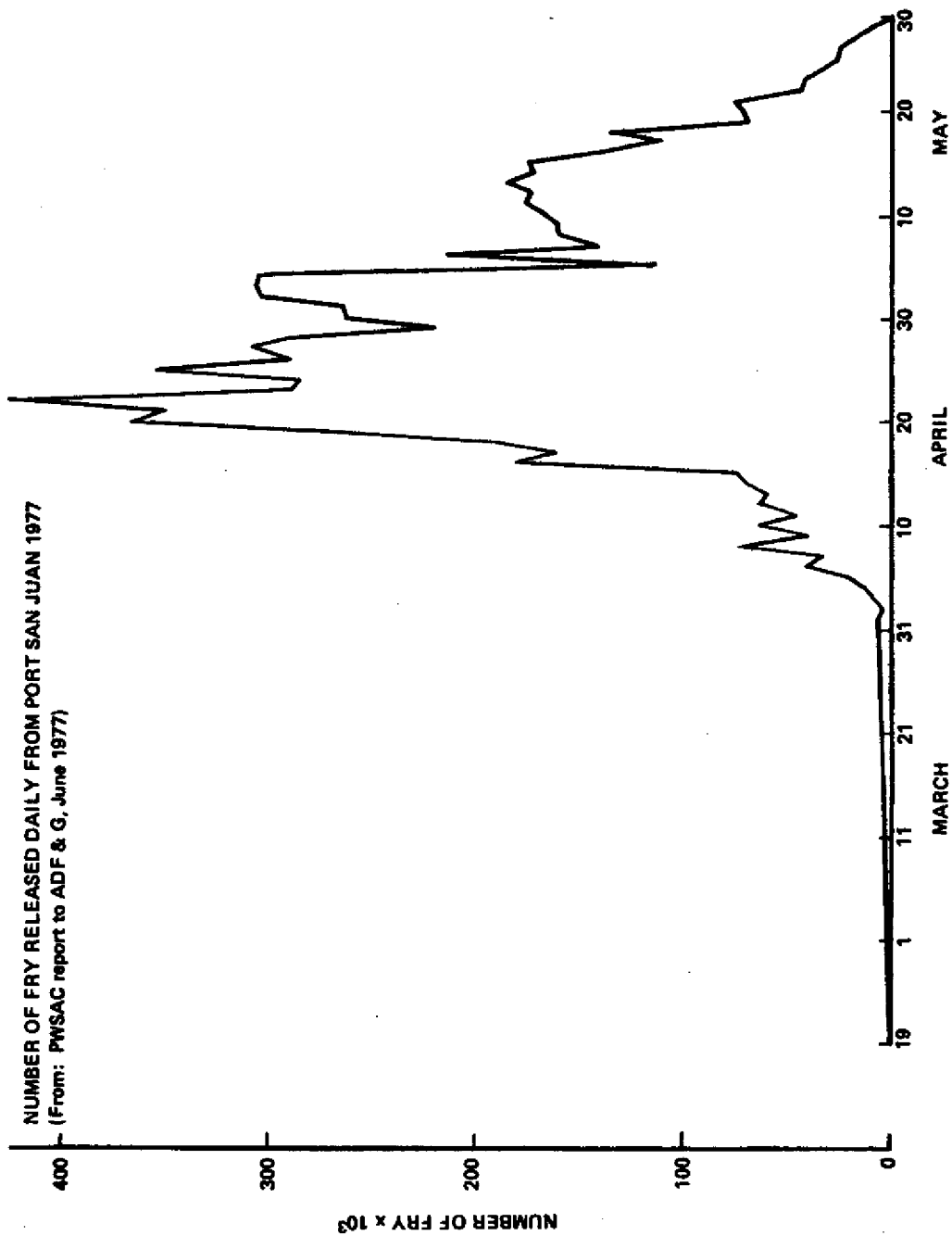


Figure 5. Estimated daily release of fry from the Port San Juan hatchery, 1977.

million eggs were placed in the astroturf incubators. PWSAC reported hatching was completed by January 31, 1977, and that survival of the "eyed eggs" to that point was about 97 percent.

Hatchery personnel estimated that about 10 million fry were subsequently released into Sawmill Bay during the late winter and spring of 1977. This number indicates 68 percent of the eggs processed by the hatchery or nearly 90 percent of the "eyed" eggs survived to become emergent fry. According to Bams (1972), Baily and Heard (1973), these figures are quite reasonable and represent an indication of substantial success for a modern pink salmon hatchery. Some inaccuracies may be present in daily outmigration as given by Figure 5 due, in part, to the tendency for pink salmon to emerge at night (McDonald, 1960; Neave, 1955). The numbers of fry actually counted and released during the day probably underestimated the numbers of fry that were allowed to release themselves at night. Errors in the figures for daily outmigration also stem from unsuccessful attempts to restrain fry during those periods when sample counts of outmigrating fry were made. The depiction is a reasonably accurate representation of relative daily fry releases.

Beginning 3 May 1977, PWSAC began transferring nearly all emerging fry into saltwater rearing pens (see Appendix I). A total of 1.5 million fry were loaded into these pens between this date and May 14. Here they were fed for approximately one month before being released. This experiment provided data on relative growth rates and experience with artificial feeding of fry. Because this special study essentially stopped the introduction of newly emergent fry into Sawmill Bay for a well defined period, our research team was able to determine the probable residence time of fry in the Bay. The results led us to extend our

search for pink fry nursery areas, and to gather additional information concerning the path the fry took in getting to sea.

Fry Migrations

In general we feel it is safe to divide patterns of fry behavior related to migration and feeding observed at Evans Island during April, May, and June into three categories: (1) those observed in Sawmill Bay immediately following release, (2) those observed within the island nursery areas, and (3) behavior adopted suddenly in June after the fry abandoned the nursery areas.

Most fry entering Sawmill Bay quickly formed small schools and moved rapidly out of the bay into the waters of Elrington Passage and beyond. Within a day or two, these fishes were congregating in numerous quiet coves among the islands and along the shore of the northern end of the passage (Fig. 6). Once established within a "nursery area" most schools would remain there several weeks. Although the possibility of fry interchange between schools at different locations was not examined, it was clear that the small fishes readily crossed deep water channels to reach the more remote island coves.

Early in June the schools of fry found in these areas quite suddenly changed their behavior, often completely leaving the nearshore zone overnight. It appeared that once the pink fry reached approximately 60 to 70 mm in length the shallow areas no longer satisfied their needs. Although pink salmon have evolved to the point where a specific smolting stage is unnecessary, Hoar (1976) feels this change in behavior may be related to a remnant of this physiological process. Following this marked behavioral change, the young pinks were consistently found farther offshore,

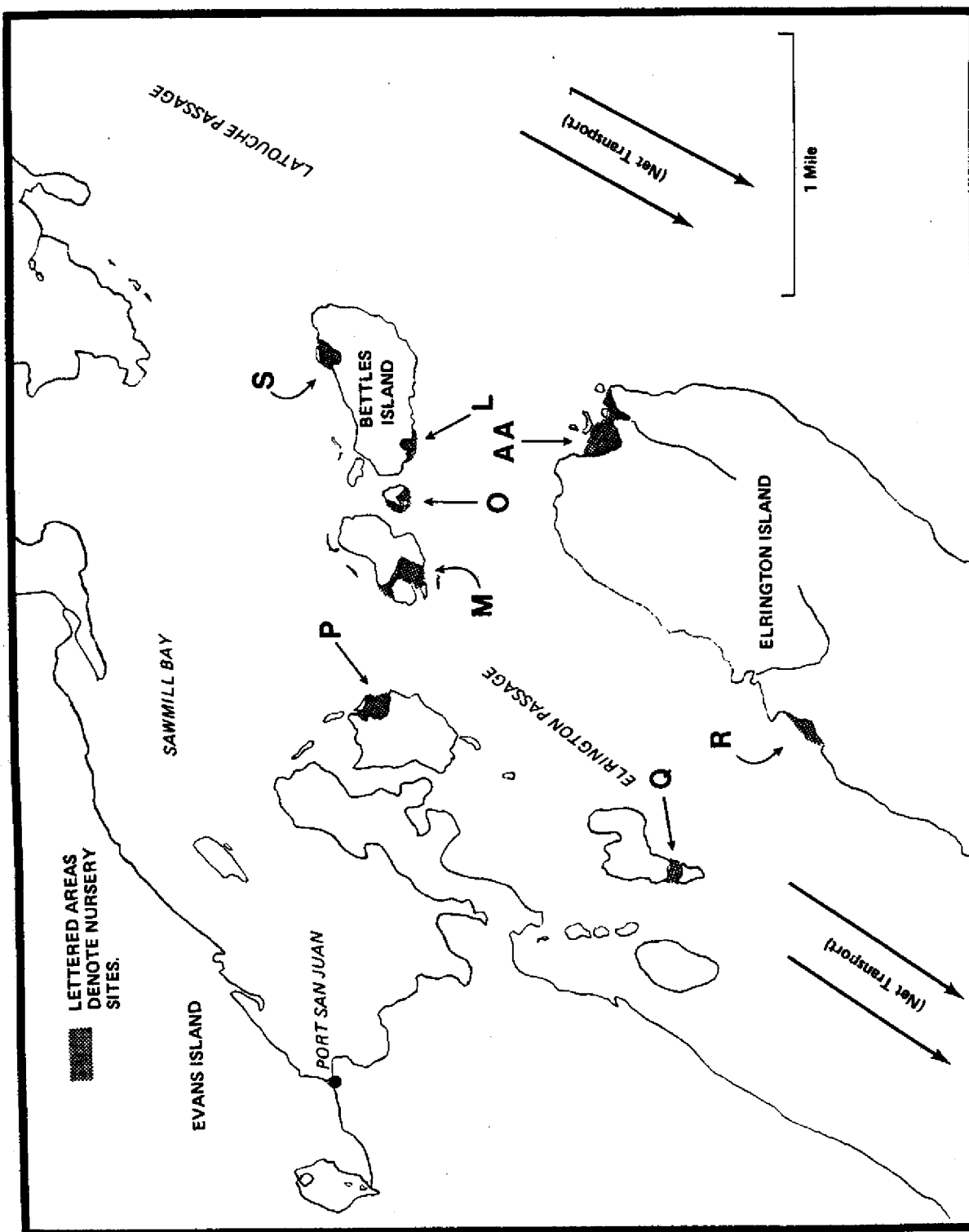


Figure 6. The location of nursery areas adjacent to Sawmill Bay and the Port San Juan hatchery, 1977.

usually holding position within a current over deep water. We feel this movement is primarily in response to feeding adaptations related to increased metabolic requirements (LeBrasseur and Parker, 1964). At this time, rather than scattering across the surface to avoid capture as they had in nursery areas, the fry would consistently dive and move into deeper water. With time these schools could be observed farther from shore often with individuals noticeably leaping clear of the water. This was the sampling situation we faced when our study ended on July 1. At that time, those few fry that could still be captured were frequently in excess of 100 mm in length. During a return trip to Evans Island in early August, an examination of the area indicated the fry had gone to sea.

Unlike pink salmon fry migrating down the Bella Coola River to British Columbia's coast described by Healy (1967) and Parker (1965), those leaving Port San Juan have only about 10 km to travel before they reach the Gulf of Alaska and open ocean. As indicated above, the young fishes apparently do not need to move very far from the hatchery before environmental conditions suit their immediate needs.

Figure 7 depicts our present understanding of the main paths taken in getting to sea by fry leaving the Port San Juan facility in 1977. This model is based upon observations of the locations of fry concentrations noted within the vicinity during the months of April, May, and June, and a general knowledge of the net flow of tidal currents in Prince William Sound. Elrington Passage contained many times more pink salmon fry during this period than any other nearby body of water, especially along its western shore. Of the factors potentially affecting the direction of migration, salinity, net tidal flow, food gradients, and celestial cues are proposed as important (Healy, 1967).

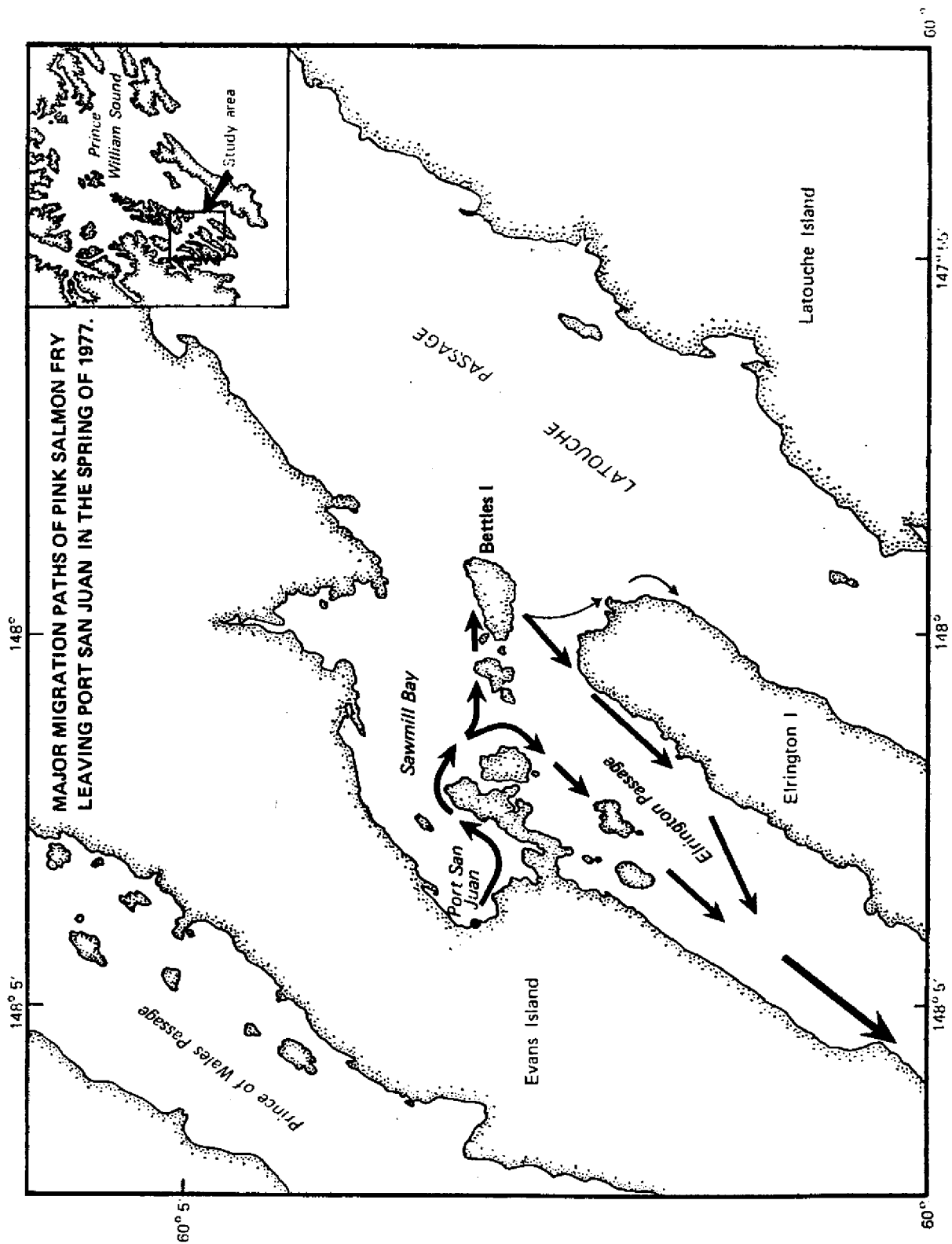


Figure 7. Probable migration routes taken by fry released from the Port San Juan hatchery, 1977.

Pink salmon emerge from the gravel as small silvery pelagic fishes (Hoar, 1958) with well known preferences for waters more saline than those of their home streams (McInerney, 1964). It may be that the initial migration of fry out of Sawmill Bay is a response to surface freshwater even though the water in the bay at our hydrographic stations consistently ranged in salinity from 26 to 29 ppm. Once outside Sawmill Bay, salinity differences are not considered very important stimuli in determining the movement of fry down Elrington Passage. Our hydrographic data also indicates the waters of the Passage are well mixed and frequently exchanged by tidal action. Although McInerney (1964) suggests pink fry use salinity gradients to orient their migrations down coastal inlets, it remains to be seen whether such a gradient exists between the head waters of Elrington Passage and the Gulf of Alaska.

The general pattern of tidal currents may help explain the migratory path taken by pink fry leaving the Port San Juan area in June. Schmidt (1977), has proposed a circulation model for Prince William Sound in which he hypothesizes a net flow of water from the Alaska Current into the Sound through Hinchinbrook Entrance. Continuity requires a subsequent outflow through Montague Strait and the southwest passages. If this notion is correct, more water flows south through Elrington Passage, on the average in 24 hours, than to the north. When the pinks move offshore with increasing size, some passive transport undoubtedly occurs. However, the larger fry outside the nursery areas were often observed to breast currents of 2 to 3 km per hr.

Another possibility is that fry follow food gradients along their migration routes. Although the hatchery fishes initiated their feeding on harpacticoid copepods while moving through Sawmill Bay, the bay itself

for reasons not particularly evident, did not appear to support large numbers of first feeding fry. Once in the nursery locations, it seems unlikely to us that the fry were abundant enough to be grazing the zooplankton community down to a point where it would be necessary for them to search elsewhere for food. This is especially true in view of the tidal currents and frequent exchanges of water masses containing clouds of passively driven zooplankton.

Sunlight and the angle of declination may be the stimulus orienting these early salmon migrations. It provides a consistent cue, and of the four factors being considered is one which could conceivably direct the fry toward the open ocean in a strictly non-random way (Healy, 1967). Johnson and Groot (1963) have described sockeye smolts as being capable of time compensated solar orientation. Healy (1967) has shown pink salmon fry are better oriented on clear days than on cloudy days. This past spring at Evans Island there was some early evidence that the fry leaving Port San Juan used the sun in selecting nursery sites. It appeared that nursery sites near Bettles Island with sunny southern exposures (L, M, O, and Q) were the first areas to be occupied (Fig. 6). Later as the season progressed and the sun angle increased, previously shady areas, such as S, P, and AA were seen to support fry.

Since there is no way to evaluate the possible interactions of these factors, we cannot objectively rank their importance. It is clear the fish preferred the island habitats over the inside waters of Sawmill Bay, and that they remained in these so called "nursery areas" for several weeks. Our observations also indicate that a radical change in behavior occurs with size. After 60 to 70 mm in length is achieved, the fry become very mobile and move away from the shallow protected nearshore environments.

We suspect a combination of many factors, some of which we may have no knowledge as being responsible for stimulating the large scale movement of "smolting" pinks toward the open Gulf of Alaska in late June and July.

Nursery Areas

By the first of May the field party was aware that large concentrations of fry could be consistently found outside Sawmill Bay. Swirling circular schools of pink fry were seen in various protected, shallow coves among the islands and along the shore of the northern end of Elrington Passage. Prior to that time, a number of sites had been selected for periodic observation. Visits were made every two to three days thereafter and by the second week in May, nine sites were being routinely monitored. For several of these coves, more than five weeks were to pass before the pink fry would leave as juveniles. From late April through the first week in June fry were seldom seen in large concentrations anywhere but within these protected areas. Those few observed elsewhere were usually moving along a shoreline. The large schools of fish were initially quite site-specific, reliably found within a few tens of meters of the same spot. Later as the fishes increased in size the schools became more mobile, and harder to catch, although they usually remained within the boundaries of the coves. In many instances more than 100,000 fry were seen schooling at locations that were often no more than a few hundred square meters in area. In early May most of the fry within any cove were of the same size as those being released by the hatchery, 30 to 35 mm. By the first few days in June they ranged in size from 40 to 70 mm.

We choose to refer to the coves indicated in Figure 6 as nursery areas because of their obvious importance to fry survival and growth.

A number of authors have described pink salmon fry migrations to "salt-water nursery areas", and it is known that initially pink fry stay close to shore, form schools that generally stay on the surface, and swim in a circular manner (McDonald, 1960; Healy, 1967). Healy (1967), in discussing pink fry from the Bella Coola River migrating down Burke Channel, describes their movement as saltatory: "The fry may spend a day or two days actively migrating - then migration stops and the fish hold up for several days in quiet bays and backwaters." Parker (1965), in another discussion of pinks from the same river, describes a continuous down-channel movement. When mention is made of saltwater nurserys these authors apparently conceptualize an entire estuary with random schools of feeding pink fry moving through it. So far as we know, small site-specific estuarine nursery areas supporting large numbers of pink salmon fry for several weeks have not been described.

Without a quantitative census of the nursery areas we cannot say with any certainty what percentage of the fry released from the hatchery actually took up residence in the island habitats. It is possible that only a fraction of the overall release stayed in the shallow areas while the remainder schooled offshore in the larger passages. Also, without having a marked population of fish to work with, our interpretation of residence time must be based on growth data. It is apparent from most size frequency distributions that recruitment to the nursery areas was continuous; periodic losses to these sites cannot be ascertained except for the case (as previously noted) related to mass "smolting" at the 60 to 70 mm size in early summer.

Fry Feeding

Details of the feeding biology of fry lie at the crux of the problem of carrying capacity. Rapidly growing fry require large quantities of food beyond that necessary for basic metabolic needs. Not all organisms in the water or on the bottom are equally nutritious or available. Most particulate matter in the ocean is non-living detritus and the living portion is dominated seasonally by microplankters which are too small to be seen or easily ingested by salmon fry. Thus these small fishes rely on short food webs, feeding on the tiny pelagic or benthic animals which obtain their nutrition from detritus or plant plankton sources. This dependency means that quite often lag times appear between the occurrence of the plant communities and large numbers of small second order consumers. The spring phytoplankton "bloom" usually begins because, in addition to availability of light and nutrients, the zooplankton grazing community which overwinters in low numbers are unable to crop the plants as photosynthesis begins in earnest. It is only after the overwintering grazers are able to feed and reproduce that the animal plankton communities increase in size. In contrast, some grazers have evolved reproductive strategies in which overwintering adults carry sufficient energy reserves as lipids to allow reproduction prior to the bloom, and the subsequent progeny occur in the water before the plant communities begin their rapid growth in the spring. In these situations, the coupling between the grazing community and the primary producers is close, and in some instances (the open north Pacific Ocean) the spring bloom is almost completely controlled.

Our concern at Port San Juan was that the scheduled large releases might lead to serious competition among fry for food that might then limit

growth and subsequently affect survival. As we mentioned previously, the literature describing natural fry feeding in estuaries hints that initially the small fishes utilize epibenthic (near bottom) copepods which draw from a benthic detrital food web. The problem here is that because the fry feed in shallow water they would be restricted in this type of feeding to a narrow strip of bottom along the beaches. If indeed this habitat were critical, then carrying capacity would be directly related to the amount of nearshore seabed supporting the appropriate food items which was also be available to the shallow feeding fry.

The results of our field study this past spring indicate that except for a few instances, epibenthic copepods (Harpacticoids) played a consistently small role in the diet of the actively feeding fishes. Table 1 lists the average number of food items in the stomachs (foreguts) of small samples of pink salmon fry taken in the nursery areas beginning in early May and continuing through late June. Except for the largest fry (82 mm), Calanoid or pelagic (i.e., floating in the water above the bottom) copepods were always the preferred food item although the diversity of the diet appears to increase with the size of the fish.

A more complete description of food items indicates that within the calanoid copepod group, one genus of abundant small copepods, *Pseudocalanus*, is important for the smaller fry (Table 2). As the fish grow, the larger copepods, particularly *Metridia*, as well as other pelagic taxa are selected. To measure feeding selectivity as well as standing stocks of food, surface net tows were taken through schools of feeding fry routinely in the nursery areas. In the data we have examined so far, we see practically no difference in the diversity of categories taken by the nets and the fry; a few items are ingested by the fishes that do not consistently appear in

TABLE 1. The relationship between fry size and stomach content measured at locations Q and P between 5 May and 25 June, 1977.

Date	Number of Fish	Average Length	The Average Number of Food Organisms per Fish										Chaeto- gnaths
			Calanoid Copepods	Harpacticoid Copepods	Cladocera	Ostracods	Euphausiids	Crab Zoea	Nauplii	<i>Oikopleura</i> sp.	Pteropods	Insects	
5/ 7/77	10	35.2 mm	29	2	-	-	-	1	-	-	T	T	T
5/19/77	10	41.1 mm	74	4	-	-	-	1	-	-	T	-	T
6/ 6/77	10	49.4 mm	65	4	1	2	1	-	T	14	T	-	T
6/25/77	10	81.9 mm	74	18	16	-	1	T ¹	1	163	3	-	T

¹T-trace, defined as fewer than 1 item per stomach.

TABLE 2. A detailed listing of food organisms taken from pink salmon fry sampled at locations Q and P four times during the spring and summer, 1977.

Food Organisms	Average Number of Items per Stomach			
	7 May	19 May	6 June	25 June
Copepoda				
<i>Metridia lucens</i>	T ¹	T	14	23
<i>Metridia okhotensis</i>	3	1	33	35
<i>Metridia</i> spp.	-	6	6	25
<i>Calanus plumchrus</i>	2	2	2	-
<i>Calanus cristatus</i>	-	-	T	1
<i>Calanus marshallae</i>	-	1	1	-
<i>Eucalanus b. bungii</i>	-	-	-	1
<i>Pseudocalanus</i> spp.	19	37	8	-
<i>Oithona similis</i>	-	1	8	-
<i>Oncaea</i> sp.	T	2	T	T
<i>Centropages abdominalis</i>	-	-	T	3
Unidentified monstrilloid	-	T	T	-
<i>Acartia longiremis</i>	-	T	-	-
<i>Microcalanus</i> sp.	-	T	T	-
Unidentified harpacticoid spp.	2	5	3	-
Unidentified copepods	5	18	39	28
Copepod nauplii	T	-	4	-
Other				
Hydromedusae	T	-	-	-
Crab zoea	1	1	-	-
Barnacle nauplii	T	-	-	-
Euphausiid furcilia	T	T	T	-
Euphausiid calyptopis	1	-	2	-
Polychaete larvae	T	T	-	-
Insects	-	4	2	T
<i>Evadne</i> sp.	-	-	-	11
<i>Fritillaria borealis</i>	-	-	T	3
<i>Oikopleura</i> sp.	-	-	13	131
<i>Limacina helicina</i>	-	-	T	3
Unidentified egg	T	-	3	T
TOTAL ²	33	78	138	264

¹T=trace, defined as fewer than 1 item per stomach.

²Exclusive of trace organisms.

the net tows (Table 3). Also, there does appear to be evidence for numerical selectivity by the fry for certain food items. The tiny, and often abundant, copepods of the genus *Acartia* and *Oithona* are probably either too small or agile to be easily ingested. The absence of *Metridia* in zooplankton samples taken on 6 and 25 June is probably an artifact of subsampling.

In summary, our preliminary information concerning the feeding of fry in the nursery areas indicates the small fishes feed opportunistically, taking items from the whole of the zooplankton community present at any time. Preference for some items over others seems to be related to both size and abundance. The older fry select the larger and rarer food particles, except for *Oikopleura* which was abundant late in the season.

Fry Growth

Pacific salmon of the genus *Oncorhynchus*, have evolved the ability to go to sea at an early age. In fact, the historical success of this group seems to be based on the ability of the various species to take advantage of the tremendous quantities of food available in the estuarine and pelagic zones of the ocean. Variations in the juvenile ecology of the five varieties stem from divergent paths associated with migration to the sea. The pink salmon is considered to be the climax of this trend in speciation since it can feed within a saltwater environment immediately upon emergence (Hoar, 1958, 1976; Neave, 1958). Little or no time is spent in feeding in freshwater and once within an estuary pinks grow at a fantastic rate (Baily, 1975; LeBrasseur and Parker, 1964). Conversely, coho and sockeye fingerlings spend one to several

TABLE 3. Zooplankton standing stock in nursery areas P and Q May 7 through June 25, 1977.

Category	no/m ³			
	7 May	19 May	6 June	25 June
Copepoda				
<i>Metridia okhotensis</i>	65	6	-	-
<i>Calanus plumchrus</i>	65	14	-	-
<i>Pseudocalanus</i> spp.	392	195	380	541
<i>Oithona similis</i>	1706	276	833	2378
<i>Acartia longiremis</i>	261	138	347	1838
Unidentified harpacticoid	16	19	27	108
Copepod nauplii	16	-	87	54
Unidentified Monstrilloid	-	-	27	-
<i>Centropages abdominalis</i>	-	-	33	432
Other				
<i>Euadne</i> sp.	-	-	120	1568
<i>Podon</i> sp.	-	-	-	486
Barnacle nauplii	-	-	113	703
Barnacle cypris	8	3	-	162
<i>Noctiluca</i> sp.	-	-	-	43027
<i>Fritillaria borealis</i>	-	-	27	162
Crab zoea	8	33	-	-
<i>Oikopleura</i> sp.	57	3	347	1027
<i>Limacina helicina</i>	16	6	73	-
<i>Thysanoessa enremis</i>	-	T ¹	-	-
<i>Telmessus</i> sp.	-	T	-	-
<i>Sagitta elegans</i>	-	T	-	-
<i>Littorina sitkana</i>	-	T	-	-
<i>Pagurus hirsuticulus</i>	-	T	-	-
<i>Aglantha digitale</i>	-	T	-	-
Unidentified isopod	-	-	7	-
Euphausiid eggs	-	-	93	-
TOTAL ²	2610	693	2514	9459 ³

¹T=trace; fewer than 1 per cubic meter

²Exclusive of trace organisms

³Does not include *Noctiluca* sp.

years in freshwater before smolting at sizes the pink can attain in only three months.

The growth of pink salmon is a continuing process until the time adults re-enter their home estuaries to spawn. Instantaneous daily growth rates are usually highest during the period the fry spend in the estuary when they may more than double their length in a month or less (LeBrasseur and Parker, 1964). Using length-frequency data and the recapture of marked individuals, LeBrasseur and Parker (1964) report growth as exponential during the first 40 days of estuarine feeding. An instantaneous daily growth rate, $g_1=0.0186$, is computed by regressing fish length on time during the period the fry are increasing in size from 35 to 84 mm. Thereafter growth decreases, and three major stanzas are recognized with the adults returning at 40 to 60 cm in total length.

In 1977 many samples of fry were collected weekly from the nursery sites in Elrington Passage. Length-frequency plots of these collections indicate the fishes stayed within these areas for several weeks and grew substantially (Fig. 8, 9). However it is difficult to determine, with any great accuracy, the relative growth rates from this information since fry were recruited continually for up to 6 to 8 weeks. Also, although 20,090 fry were tagged in the hatchery during May, none have been recovered from the samples so far analyzed. A mark and recapture program would have given a much more accurate technique for measuring growth rates but many more fry would have to have been marked.

Figures 8 and 9 suggest that fry ranging in size from 30 to 40 mm increased their length by 2 to 3 mm per week in the nursery sites. Since most fish grow rapidly early in life, these values are not unreasonable, and may in fact be conservative considering the bias introduced into

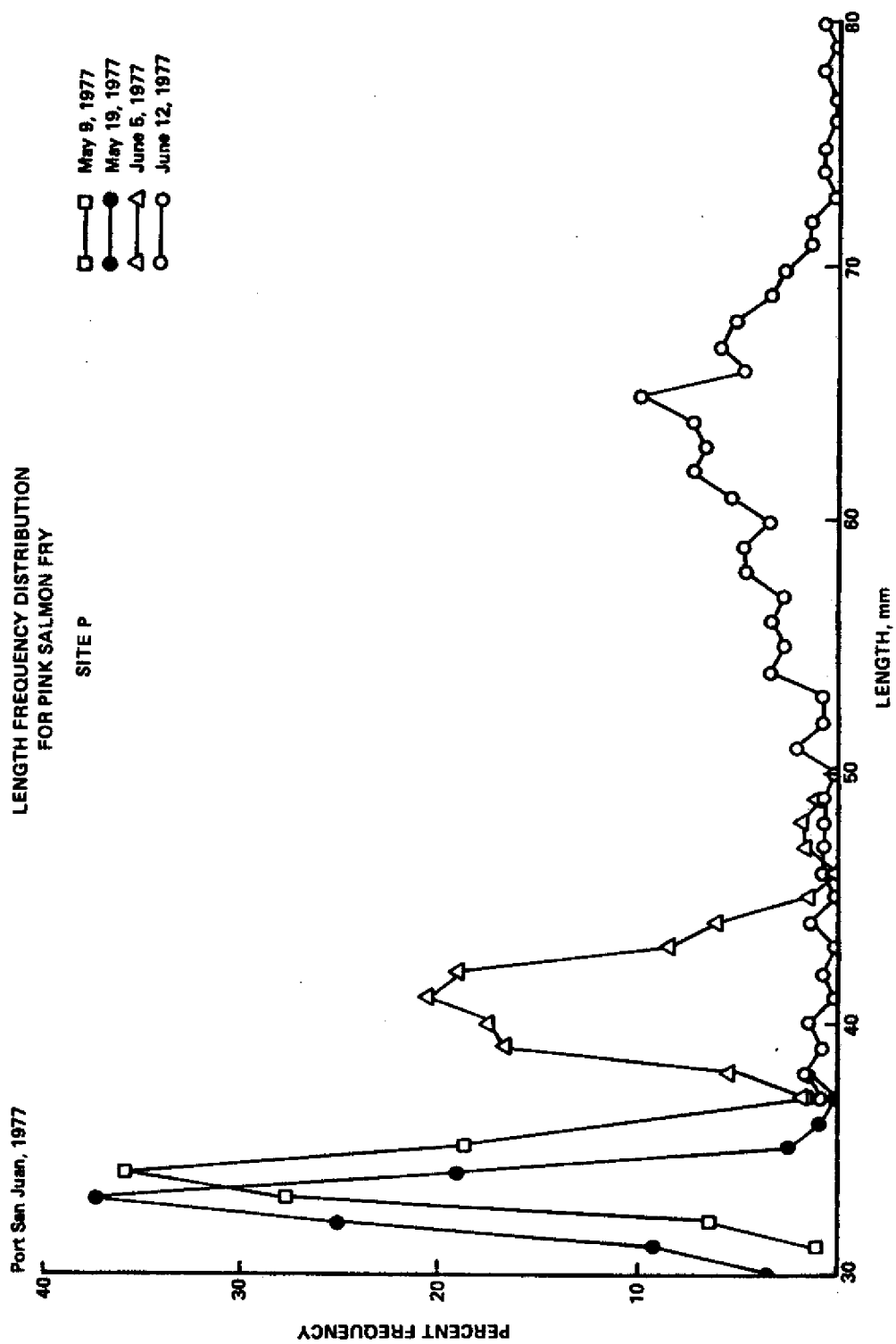


Figure 8. The distribution of sizes for pink salmon fry sampled at site P, May 9 to June 12, 1977.

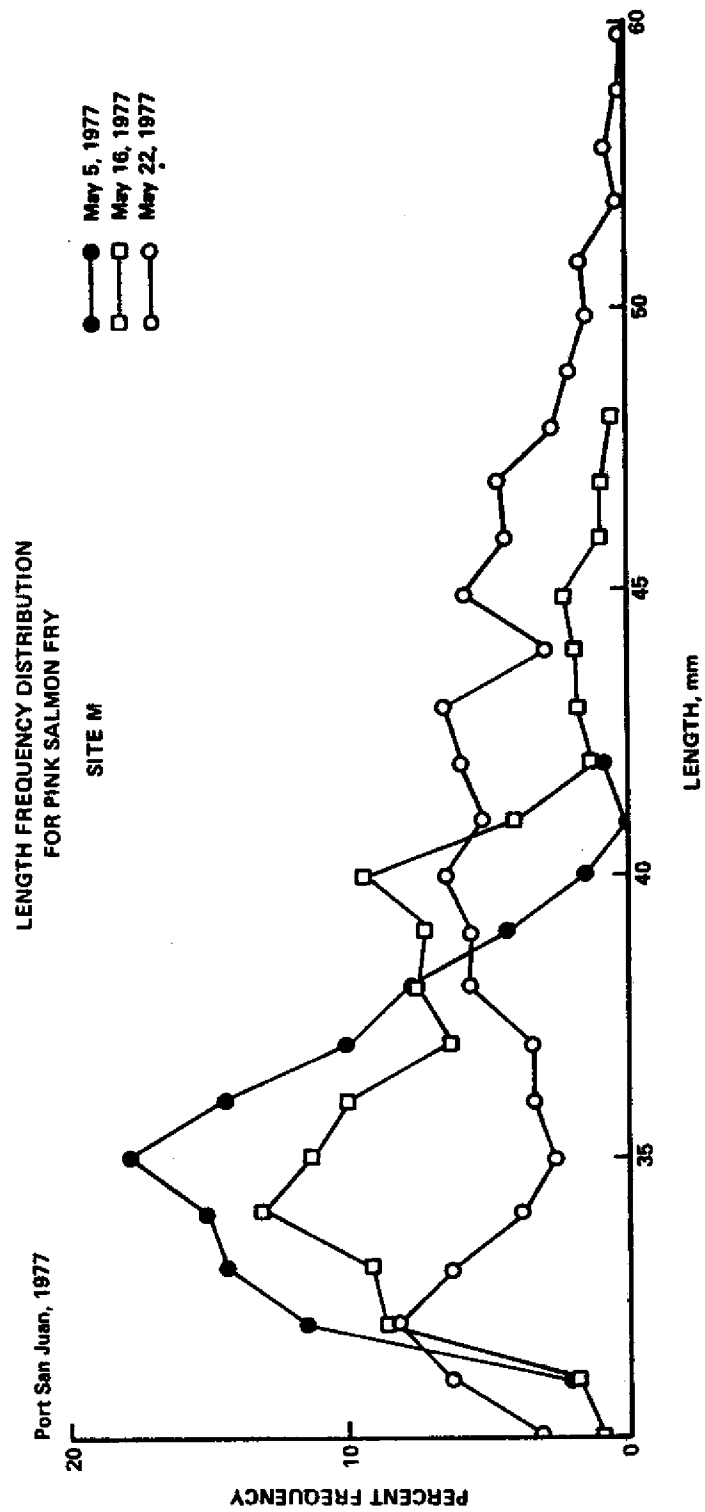


Figure 9. The distribution of sizes for pink salmon fry sampled at site M, May 5 to 22, 1977.

calculations due to continual recruitment (Weatherley, 1972). Also, fry leaving the Port San Juan hatchery may have been slow to begin their active feeding phase. We suspect this because the fry emerged to begin migration while still well supplied with yolk. As such, they were probably not in immediate need of food. According to Bams (1972) this "premature" phenomenon is not uncommon for hatchery reared pink salmon. The fry consistently emerge from rearing boxes less advanced than creek fry.

Figure 10 depicts length-frequency data for two groups of fry selected because of their nearly normal distribution of lengths, and their clear separation in time. One group consists of 184 fry taken from the hatchery and may be considered representative of all fry leaving the facility in 1977. The second group of 473 fry was taken from site W, 10 km south of the hatchery in Elrington Passage June 2, 41 days after the peak in outmigration.

Assuming that the average fish in group two left the hatchery during the peak of outmigration, a crude estimate of growth can be obtained. Using 31.5 mm as the size of fry leaving the hatchery, and 52 mm as the subsequent size sampled 41 days later at site W, a simple exponential model can be used to calculate an instantaneous daily increase in length of 0.0122. This value is considerably less than $g_1=0.0186$ reported previously for natural pinks in British Columbia waters. However, if the fry do not begin serious feeding until ten days after their release because of yolk reserve utilization, the field growth computed for 31 days rather than 41 is 0.0162 per day, not that much different from the estimate of LeBrasseur and Parker (1964).

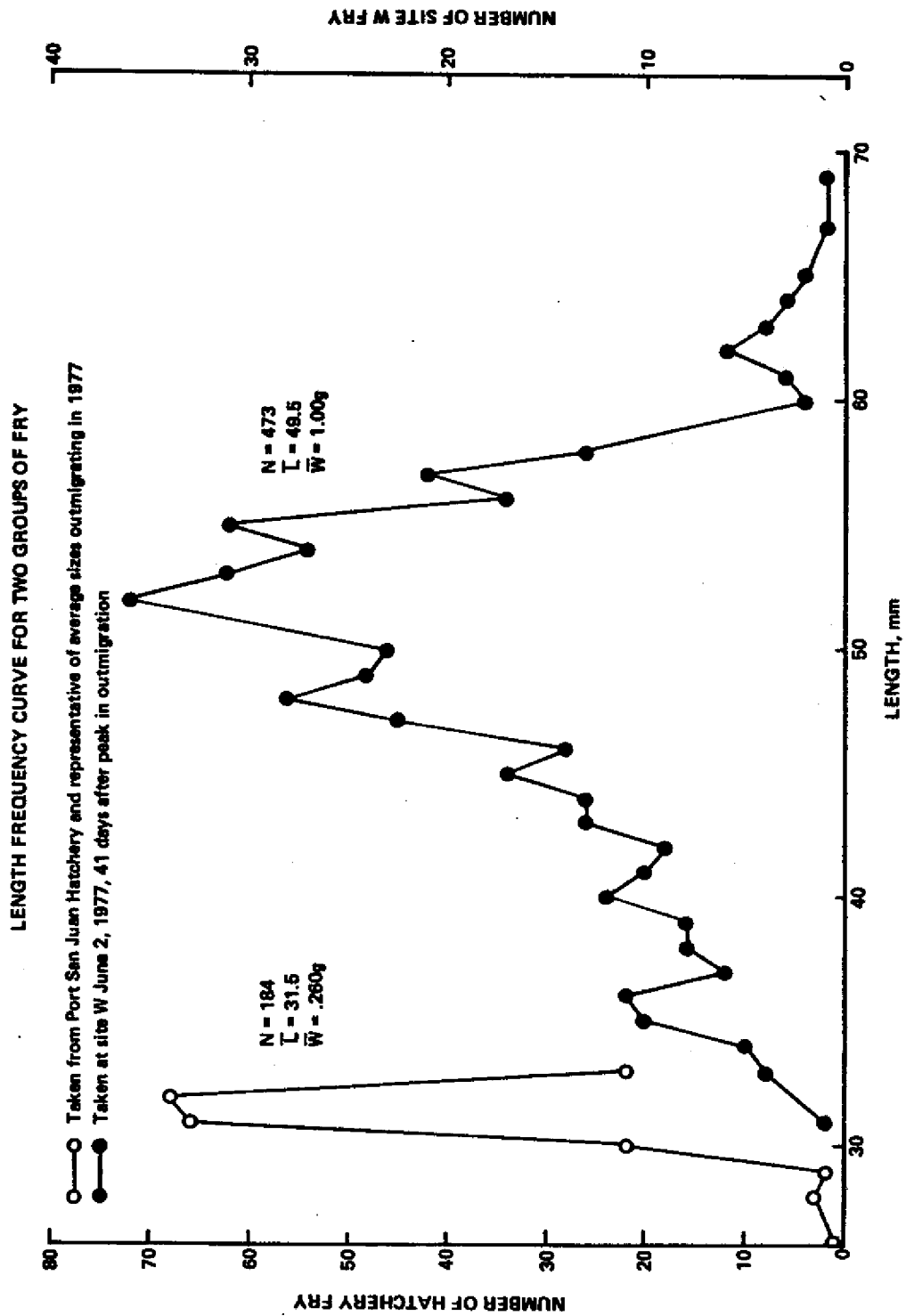


Figure 10. Size frequencies of pink salmon fry used to estimate instantaneous daily growth, 1977.

Since rate of growth is temperature dependent, the presumed cooler waters of Prince William Sound could have made the difference. We also found that fry leaving the hatchery on April 22, averaged about .26 gms each and were nearly four times heavier 41 days later. This corresponds to an 0.78 gram increase in weight for the period.

Predation and Competition

Parker (1965) has shown that for pink fry entering the sea, more than 75 percent may die within the first 40 days. Many juvenile fish are thought to go through a "critical period" during which they must find and obtain their first food (May, 1974). If during this period food is not encountered, mass mortality and poor recruitment of the year-class into the fishery results. However, pink and chum salmon are relatively large (30 to 36 mm) when they enter the sea. It is unlikely that they experience such a "critical period" because of the generous amounts of yolk with which they are supplied. Moreover they are capable swimmers and can go a long distance in search of a first meal. It is more likely predator activity accounts for the large numbers of fry removed from these populations (Hunter, 1959). Our observations in 1977 tend to support this latter speculation.

Coho salmon, dolly varden char, cut-throat trout, steelhead trout, and various sculpins are species commonly reported to prey upon pink and chum fry (Hunter, 1959; Parker, 1971). For fry leaving Port San Juan in 1977, the Pacific tomcod, *Microgadus proximus*, presented the only serious predator problem we observed. Tomcod were present in large numbers within Sawmill Bay where they fed heavily upon fry that were being released. Although no routine attempts were made to calculate the numbers of fry eaten

by tomcod within the bay, we feel it must have been a significant fraction of the total number released.

On April 23, 296 tomcod were caught just offshore near the point of outmigration with one set of a 100-ft beach seine. Twenty-five of these fishes were measured and their stomach contents examined. The tomcod ranged in size from 16 to 30 cm and 16 were found to contain from one to 19 fry. For the 25 examined the average was 3.5 fry per stomach. Hind guts were not examined.

A simple calculation reveals that if 5000 tomcod (a first-order guess) consumed 3.5 fry per day for a month, over half a million fry would be taken, or 5 percent of the total number released in 1977. During April and May we estimate by observation at least that number of fishes were schooling in Sawmill Bay near the hatchery. We also feel 3.5 fry per day to be a conservative estimate of the rate at which individual tomcod were feeding on fry.

No predators were seen within any of the island nursery areas. Eleven species of birds were seen presumably taking fry but only within Sawmill Bay, especially near the point of outmigration. The following is a list of those species:

- Harlequin ducks - *Histrionicus histrionicus*
- Buffleheads - *Bucephala albeola*
- Common Merganser - *Mergus merganser*
- Redbreasted Merganser - *Mergus serrator*
- Belted king fisher - *Megasceryle alcyon*
- Glaucous wing gulls - *Lagur glaucescens*
- Pelagic cormonants - *Phalacrocorax pelagicus*
- Arctic tern - *Sterna paradisaea*
- Surf scoter - *Melanitta perspicillata*
- Mew gulls - *Larus canus*
- Black-legged Kittiwake - *Rissa tridactyla*

None of these birds were killed and examined but it is unlikely they made inroads on the fry population as great as those made by *M. proximus*.

In 1977, 14 samples of various species of fish other than pink salmon were collected. In all cases these samples were obtained while attempting to collect fry. While we do not yet know the total number of different species included in these samples at least six were found schooling with the pink fry during May and June. These include the Pacific sand lance (*Ammodytes hexapterus*), juvenile Pacific herring (*Clupea harengus*), juvenile Pacific tomcod (*Microgadus proximus*) as well as three presently unknown species of juvenile rockfishes.

These six species were seen and sampled on several occasions while they were schooling with pink salmon fry both within the nursery sites and after the fry left those areas. The possibility exists, of course, that these fishes may have been serious competitors with the fry for food. Our opinion however, is that they were not since food abundance did not appear to be a limiting factor in 1977 and because most of these species did not appear until the fry were rather large and accomplished swimmers. Conversely, it may be that the other species suffered as a result of the introduction of the large numbers of pink fry. Juvenile tomcod, *M. proximus*, was the one species found most frequently in association with the pink fry. It may be tomcod are increasing their numbers in and near Sawmill Bay because of the added nutrition they are obtaining from hatchery fry.

Pen Feeding and Growth Experiments

In 1977, five experiments were conducted that involved holding fish in floating pens. By placing fry from the hatchery in small enclosures moored within Sawmill Bay or cove M we hoped to gain information on feeding behavior, prey selection, and rates of growth, digestion and

starvation. The pens were made of either 1/8-in mesh nylon netting or 0.158 mm mesh nitex, and were suspended from plywood or PVC pipe frames. Polystyrene foam was used for flotation (see Appendix I).

Experiment #1; Growth on natural plankton

For this initial experiment, 210 hatchery fry were placed in a 1 m³, 1/8-in mesh pen moored in about 7 m of water (low tide) next to the hatchery at the southend of Sawmill Bay. Beginning on April 21 and extending through May 2, fry were removed daily from the pen for measurements of length and stomach content analyses. On April 21 the fry averaged 32.4 mm fork length; 13 days later they had grown to 33.8 mm. In addition, it was obvious that by May 2 the fry had also made significant gains in weight, although the weights of fishes were not taken.

The stomach analyses revealed that all fry began the experiment with empty stomachs and that each possessed varying amounts of residual yolk. By day seven most of the fry were eating tiny organisms moving through the pens with the current. Subjectively their stomachs were usually found to be 10 to 20 percent full, occasionally more than that. The number of food particles within an individual stomach was definitely inversely related to the amount of yolk remaining. Those with less yolk consistently had more food items. By May 2 some fry were still found with yolk remnants and very few natural food items.

Although constrained by the net to the surface water, these fry were found to feed on the same variety of organisms as were the fry swimming freely through Sawmill Bay. Harpacticoid copepods and barnacle cypris larvae 1 to 2 mm in length, were by far the most commonly consumed food

organisms. Two important points concerning this diet should be mentioned: (1) Although harpacticoid copepods are usually considered benthic organisms tied to a detrital food web, the small pinks were feeding on them at the surface. This point needs further investigation, since the literature notes that salmon feed on harpacticoids which implies the organisms are taken on or near the bottom; (2) Neither the barnacle cypris stages nor the harpacticoids were the most abundant members of the zooplankton community. This suggests the fry were feeding selectively and were attracted for some reason to these two organisms. After viewing living zooplankters through a microscope we feel that the attraction to the barnacle larvae and harpacticoid copepods was related to their activity and color. The cypris stage is constantly moving while the small copepods were a colorful red and also very active.

Water temperatures at the time of the first experiment ranged from 6° to 8.25° C. Because of low temperature and reduced sunlight associated with water during this period, algal growth and clogging were not a problem with the pens. Zooplankton did pass through the netting and the fry were able to feed. If this experiment had been extended another ten days, some significant growth information may have been obtained. Unfortunately after 11 days the experiment was arbitrarily terminated; the remaining fry were transferred to another pen for a second experiment.

Experiment #2; Rates of digestion

The second experiment was designed to determine the residence time of food in the guts of fry that were known to have been feeding. A second pen of 1 m³ and 0.158 mm mesh was used. The 90 fry remaining

from the first experimental pen were transferred to this food-free environment. Beginning at 13:00 hours on May 2, five fry were removed every few hours and the contents of their stomachs analyzed. After nine samples were collected 25.5 hours later, a sample of five fry was found containing no food. This experiment indicates that between 20 and 24 hours are required to digest and move food through the gut of the early released fishes.

Experiment #3; Starvation

The third experiment was designed to determine the length of time fry taken from the hatchery could survive without food. One hundred and fifty fry were placed in the 0.158 mm mesh pen in Sawmill Bay and kept there without food from May 5 through June 2. As above, periodic examination of the stomachs of samples of five fry were made during that time. The results revealed that the fry were unable to obtain zooplankton and were mostly empty. The fry began the experiment at an average length of 31.8 mm and approximately .210 g per individual. During four weeks without food only 20 of the 90 fish died, 14 of these in the last nine days. The experiment was terminated because fry still alive on June 2 were feeding on algae growing inside the pen as well as on the bodies of fry that had died since previous examination of the pen.

Although the experiment was compromised by the growth of fouling organisms, it is apparent that fry can live without traditional food for a period approaching 30 days.

Experiment #4; Growth on natural plankton, replication

The fourth experiment began 5 May and ended 2 June, 28 days later. The 1 m³, 1/8-in mesh pen was moored in the same spot as the previous

three experiments. These observations were planned as a duplication of the first experiment with the intention of holding the fry longer so that adequate growth rates might be obtained.

Two hundred fry from the hatchery at an average length of 31.8 mm and average weight of .250 g were selected. Initially, 10 fry were removed from the enclosure daily to document the time it took for feeding to begin. Later samples were collected every three to five days. By the end of the first week only half of the fry were found to contain food. Two weeks later most contained food but the time was never reached where stomachs could be said to be completely full. After two weeks the fry showed no increase in growth as had been the case in the first experiment. The most common items found in stomachs were extremely small (<1 mm) barnacle nauplii. Occasionally other items such as barnacle cypris, harpacticoid copepods, and cyphonautes larvae were seen. During the first two weeks it was assumed the fry were living on their yolk reserves. Thereafter, the condition of the fry deteriorated and by the time the experiment was terminated, the average length for 47 remaining fry was 30.1 mm and the average weight 0.159 g.

Clearly the fry had been starving even though they were able to ingest small numbers of barnacle nauplii. The physical condition of these fry appeared to be no better than those that were supposed to be starving at the same time in experiment #3. We suspect algal growth on the net caused problems with this experiment preventing most food particles from reaching the fish. Temperatures in the water ranged from 9° to 12.25°C, and the days were frequently quite sunny. In addition, this was the time of a decrease in zooplankton concentrations following the peak which had been reached the beginning of May (Fig. 4).

Experiment #5; Growth on natural plankton in the nursery areas

The last experiment represented an attempt to gain information on growth rates in waters outside Sawmill Bay. A 1.5 m³ net was constructed of 1/8-in mesh nylon netting and moored at site M in 3 m of water (low tide). On May 15, 3,700 fry were taken from the hatchery and transferred to this inclosure. A subsample of 184 fishes was removed that same day for measures of size and weight (average length, 31.39 mm; average weight 0.258 g per fry). Samples of approximately 200 fry were subsequently removed for measurement every week for the next six weeks. In this way we hoped to be able to obtain a more accurate growth rate for fry living in a nursery area. During the first three weeks of the experiment, the pen was constantly surrounded by freely-swimming fry feeding at this site. However, after June 10, this cove lost its natural population and the fry in the pen were all that remained.

The results of this experiment surprisingly showed no growth after six weeks of holding. On June 27, 110 fry of those that remained were measured and the average length was found to be 32.06 mm; the average weight had fallen to .180 g. This contrasted noticeably with the fry that had vacated the nursery 17 days earlier ranging in size from 40 to 70 mm. Again algal fouling of the net is suspected even though attempts were made to clean the net on a regular basis. It may also be that these fry, unable to swim freely to their prey were unable to obtain a ration sufficient for growth. In light of the increase in size obtained from fry in the first experiment we think it more likely that clogging of the net was the principal reason the fry were unable to grow. Water temperatures were recorded continuously on a thermograph during this experiment and ranged from 6.9° to 10.5°C.

The results of the pen experiments raise some serious questions about the feasibility of holding fry in enclosures for measurements of growth on natural food. If a large mesh is used to allow food organisms to pass freely, the fry can escape. If the mesh is small enough to hold the fry, fouling soon reduces water circulation and with it the availability of food. Also, if the distribution of food organisms is patchy, and there is reason to suspect this is so, free swimming schools can move about within the nursery to intercept swarms of zooplankton, whereas the pen held fishes cannot. The degree to which active searching for food is important is not known, although it would seem to be a critical factor where small changes in depth and horizontal displacement could rapidly introduce the fry to new concentrations of zooplankton.

DISCUSSION AND CONCLUSIONS

Prince William Sound

An indication of the ability of Prince William Sound to rear pink salmon fry may be obtained by consulting the historical record of estimated total returns by year as reported for the commercial fishery, and by using some constant value of survival from fry to adult. Assuming on the average that one percent of the fry of any year return as adults the next year, during the period 1959 through 1968 Prince William Sound probably reared between 300 million and 1 billion fry with values of about 400 million occurring most frequently. Whether these limits represent real constraints on the number of wild fry that consistently may be grown by the system or other factors such as restrictions on spawning habitat is not known to us.

Approaching the problem of limitation from a theoretical vantage point using a crude tropho-dynamic model, the following additional estimates of carrying capacity can be obtained. Given that about 75 to 150 gC per m² are fixed annually by phytoplankton (J. Goering, personal communication) and further that 20 percent of this amount probably represents the total annual secondary productivity, 15 to 30 grams of carbon are available per m² of bottom as animal plankton and micronekton. Further, if half of this material is associated with organisms larger than 200 μ in size, that weigh on the average 0.1 mg (dry wt) containing 0.05 mgC each, densities of 15 to 30 x 10⁴ organisms per m² are predicted as "production" through the year. In fact, standing stocks of total zooplankton approaching 15 to 30 x 10³ organisms per m² have been reported for the Gulf of Alaska and Prince William Sound (Cooney, 1974).

If only 10 percent of the predicted animals are available to the surface feeding fry (considered the only predator on this source for simplicity) each square meter of the Sound should support 1.5 to 3.0 fry annually that consume about 100 zooplankters daily for 100 days of rearing in late spring and early summer. Multiplied by the surface area of the Sound, $8.8 \times 10^9 \text{ m}^2$, an estimate of carrying capacity in the range 13 to 26 billion fry is obtained.

It seems unlikely that only salmon fry would feed on zooplankton or that the total surface area would represent the "nursery". Rather it seems that the shoreline distance would more accurately partition the fry feeding habitat. If a strip 100 m wide running the entire length of the shoreline (3200 km) is considered instead of the whole of the Sound, the nursery area becomes about $3.2 \times 10^8 \text{ m}^2$ supporting 4.8 to 9.6×10^8 or 480 to 960 million fry annually, a figure not unlike that estimated by adult return run size with assumptions on fry survival. It is conceivable that in the nearshore zone, the fry may actually be the major consumers of zooplankton with minimal competition from other species.

It must be recognized that these calculations represent at best, estimates with order of magnitude precision. On the other hand, it would seem that an extreme upper limit of 10 to 30 billion fry is suggested if the surface of the Sound rather than the periphery is considered. Also, if the fry, in competition with micronekton (which is probably more likely), crop only 10 percent of the food available to them a figure of about 1 to 3 billion fry is indicated.

These estimates are provided as first-order guidelines for those who may be interested in deciding how many additional hatchery facilities could be added to the Sound with the expectation of the reasonable survival of both hatchery released fry and wild stocks.

Evans Island Hatchery

The study at Evans Island provided an opportunity to examine the detail of fry survival beyond the framework of crude theoretical models. It is clear from our results that not all available beach space, including numerous small embayments, were selected by fry released from the hatchery. Instead, schooling was observed to be very site-specific and apparently associated with only a small percentage of the shoreline. We interpret this finding to mean that some locations are much more desirable, for whatever reasons, than others early in the life history of the pink salmon.

This observation could prompt concern about overcrowding, competition for food, and susceptibility to predation in the nursery areas. Our study, and those of others, suggests that pink fry actively feeding during the period of early growth can consume up to 100 particles per day. The apparent paradox of high numbers of fry (several hundred per m^3) finding sufficient food at times of low zooplankton abundance has its resolution in the case of Evans Island, in terms of particle flux associated with daily tidal exchange.

By conservatively assigning 0.2 m per sec as an average tidal velocity over an 18 hr period each day, a stationary point is passed by the equivalent of approximately 13,000 m^3 of water. At densities as low as 10 food items per m^3 , this flux could support 1300 fry per square meter each eating 100 particles during that day. The important factor in this analysis is not the concentration of food at any particular time, but the rate at which it is moved through the nursery areas. In this respect, the "island habitats" represent an optimal feeding regime being situated as they are in Elrington Passage, an area of marked tidal mixing and transport. In addition to the horizontal movement of the water, tidal energy also imparts a vertical

component of turbulence which serves to renew the surface water with plankters that may normally reside deeper in the water column. A well known marine example of advective enhancement of growth is the large stands of dense "kelp" that exhibit exceedingly high growth rates in waters of astonishingly low nutrient value. Invariably these plants grow in areas of marked tidal currents where they extract nutrients from enormous volumes of water which pass them daily; none could exist in a stationary "lake" in the sea.

Therefore, one criterion for selecting a hatchery location would seemingly be access to areas of vigorous tidal exchange. This means channels and passages rather than the heads of long fjords, such as are characteristic of much of the topography of Prince William Sound. On the other hand, it appears that fry require rather specific habitat for purposes of shelter and perhaps orientation. These requirements were met most closely by the islands adjacent to Sawmill Bay in the case of fry released from the Port San Juan hatchery. It remains to be seen if the much larger release scheduled for the summer of 1978 will spread to other less preferred sites, or whether the nursery areas found this past year will absorb the increased numbers of fishes.

The problem of predation should not be completely ignored in areas away from the immediate vicinity of the hatchery. The highly populated localized nursery areas are vulnerable, but perhaps not as easily located as are the mouths of streams where dolly varden trout and tomcod traditionally congregate to feed on outmigrating salmon. Herring, rockfishes, adult pollock and cod, and perhaps smolting silver salmon are present in adjacent waters and capable of taking large numbers of fry at random times. The fact that these small fishes school near the surface provides protection from the larger predators which generally occur deeper in the water column. Losses to seabirds are also a possibility, although as noted, birds were never recorded as serious predators during the field study.

RECOMMENDATIONS

One objective of this study was to provide potential user groups with suggestions concerning the release schedule of fry in relationship to varying environmental factors such as food and perhaps temperature in a way that could provide the greatest fry survival. Although this report is based on limited information, for planning purposes we feel the data support the following recommendations:

1. Because of its opportunistic location relative to nearby areas of food availability, it does not appear advantageous for hatchery personnel to hold early emerging fry at Port San Juan or to coordinate releases with periods of high zooplankton abundance. As discussed, even with very low numbers of food organisms, the local tidal currents provide adequate particle fluxes in the nursery areas to meet fry feeding requirements. Holding fry for massive releases at times of increased abundance could overload the smaller sites and displace fishes that otherwise would remain there.

2. Hatchery personnel should routinely monitor water temperature, and food abundance and kind at a few key locations to document any unusual variations that might correlate with enhanced or reduced numbers of spawning adults returning the next year. These simple records will provide the beginning of a data base for predicting fry survival and subsequent run size.

3. The problem of predation in the immediate area of the hatchery must be addressed. We recommend releasing fry into a series of salt-water pens, holding them for a short period (five days) without feeding, and then towing the pens to a location near the nursery sites for release. We recommend against extensive artificial feeding for these short

periods since the fishes have a large yolk reserve and will not begin active foraging for a few days. Releasing fry near the nursery areas should optimize their first feeding opportunities.

4. The location of future hatcheries should be chosen carefully. It is understood that each facility requires an adequate freshwater supply. However, the importance of the estuarine receiving water must not be ignored. Critical factors to examine in areas the fry may use as nurserys are food as related to tidal exchange, shelter, and remoteness from freshwater input as related to predators. Since no two sites will be similar, it can be expected that differing strategies may have to be employed at the saltwater end of the operation to provide the greatest possible returns. Whereas rearing in saltwater pens is apparently not advantageous in Port San Juan, extended artificial feeding could become an important link in fry survival at another location. The point is that each new site will require an operational plan that exploits its natural characteristics while minimizing any environmental deficiencies. No single "cookbook" of musts would seem appropriate except in the broadest view.

FUTURE STUDIES

The problem of describing the important factors in the estuarine survival of salmon wild stock and hatchery fry is by no means a simple one. Relating marine productivity to growth beyond theoretical calculations involves an examination of food dependencies and predation that can only come through extensive sampling of fry and potential food sources phased through the season at the various sites. Much of this work is routine and could conceivably be undertaken by the private sector with minimal training. The more complex questions of interactions between wild fry and hatchery released fishes, of estuarine oceanography as it related to "food" production and advection, and the relative importance of benthic and pelagic food communities and their utilization with time requires a more specialized experimental approach and should be pursued by agencies with expertise in these areas.

PWSAC intends to build additional facilities at several sites in Prince William Sound. Of immediate interest is the Esther Lake site east of Whittier on Esther Island. In addition to pinks and chums, the corporation plans to examine the possibility of rearing red and silver salmon in the adjacent lake. This development would presumably require a limnological evaluation of Esther Lake with regard to its carrying capacity for these species in addition to an examination of the nearby estuary. This facility is planned for 100 million egg incubation capacity and as such represents a significantly larger hatchery than the one on Evans Island. As yet there have been no substantial evaluations of the area with regard to the nearby marine receiving waters or the ecology of Esther Lake. Esther Point, near the proposed site, is exposed to the south so that weather from that direction will concentrate

wind waves and swell across the entire southern face of the island. This may cause fry to seek shelter on the Port Wells side or one of the other larger embayments to the east. Nursery habitat should be evaluated there particularly as it relates to shelter for the newly released fry. In contrast, Wells Passage will probably provide more than adequate supplies of food associated with the tidal exchange, but this notion should also be documented.

Since each new site will reflect problems unique to its location, the most efficient operation of a hatchery, in terms of returning adults per unit cost, may well involve a "customized" site specific strategy for handling fry both in the fresh and saltwater phases of the operation. The studies upon which such strategems are conceived should be planned and executed during the building phase of each site to minimize trial and error once the hatchery is in operation.

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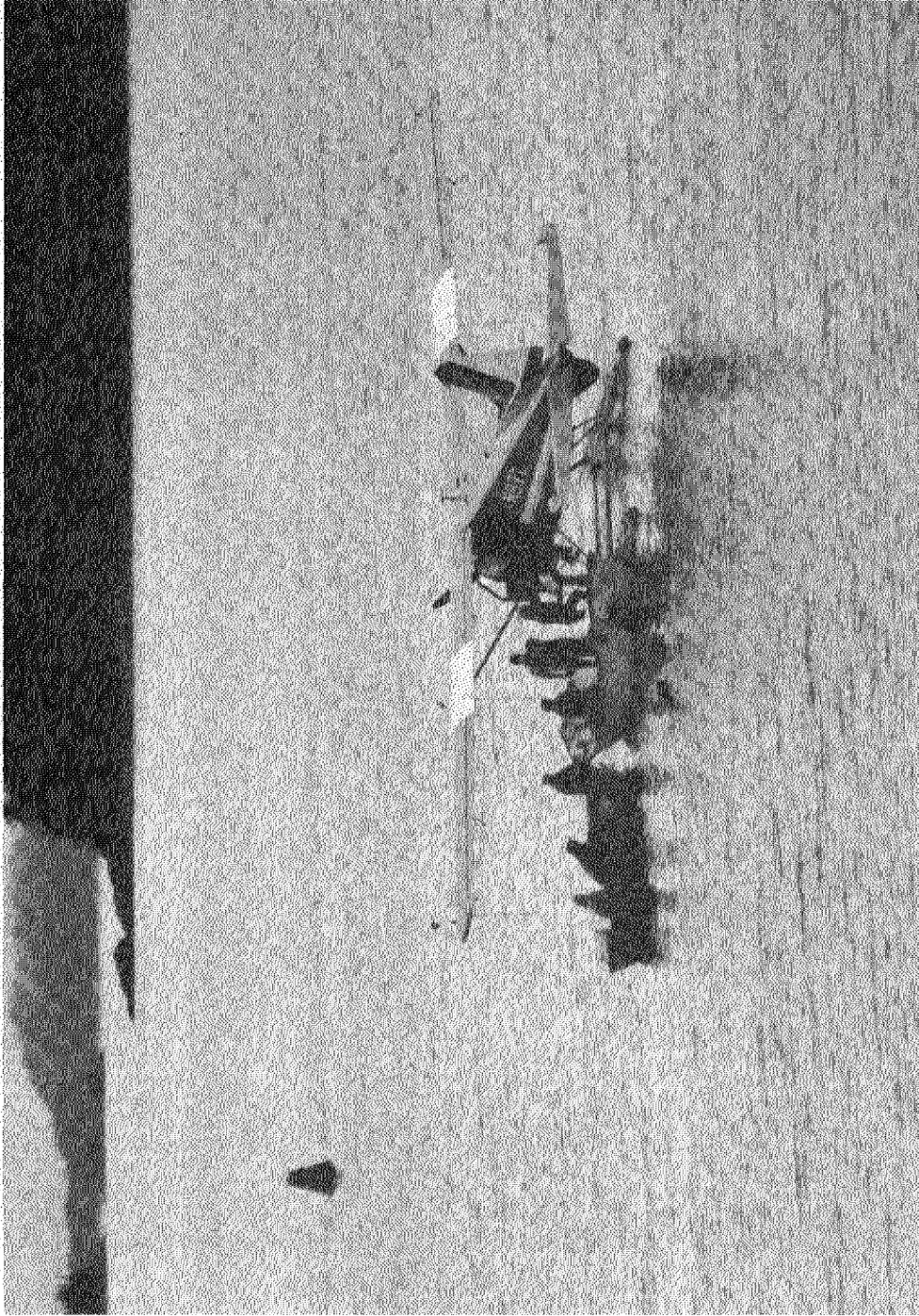
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APPENDIX I

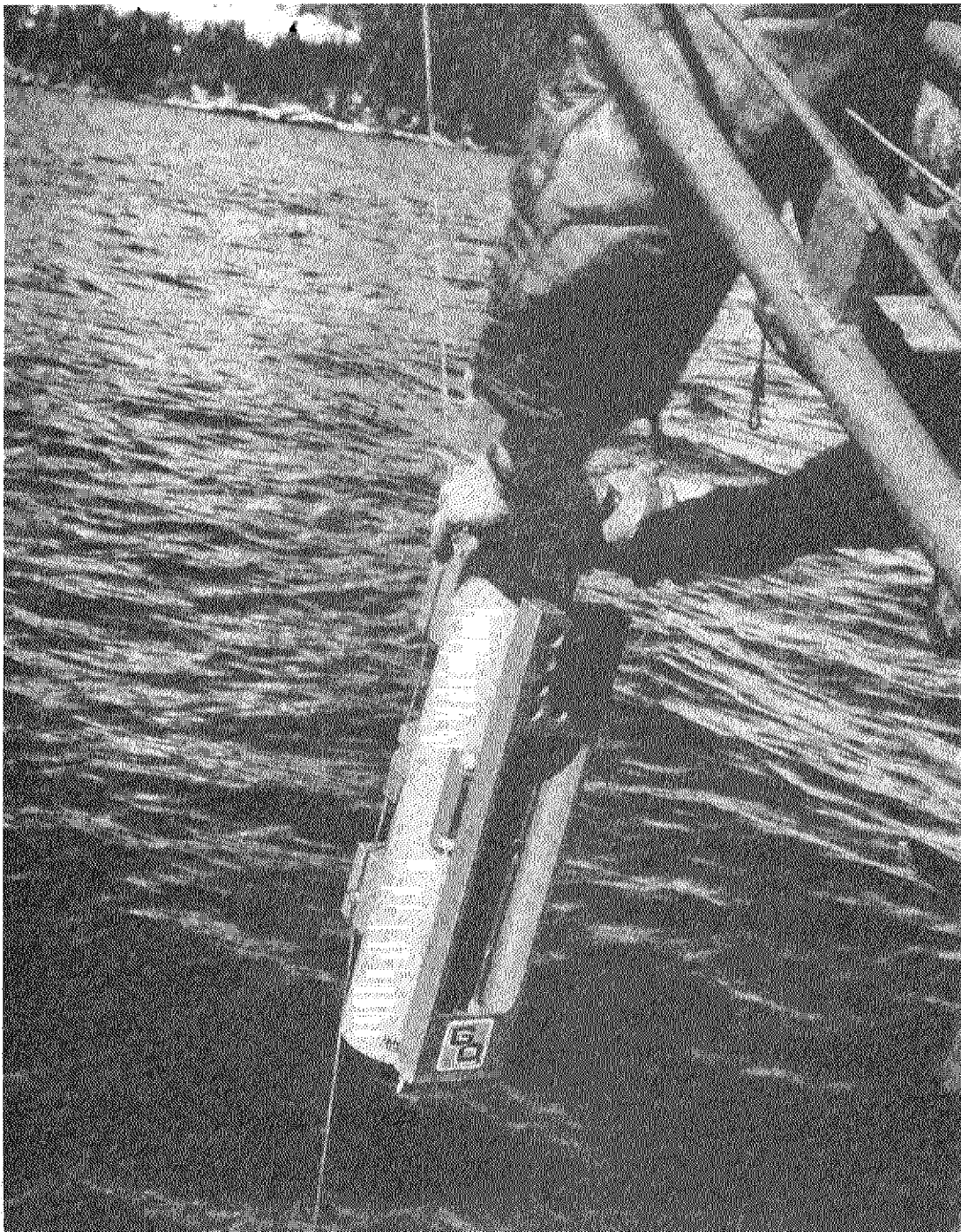
The following series of photographs taken in and around Sawmill Bay, April through June, 1977, illustrate several facets of our study. Photo credits are due Mr. David Urquhart and Mr. John Hilsinger.



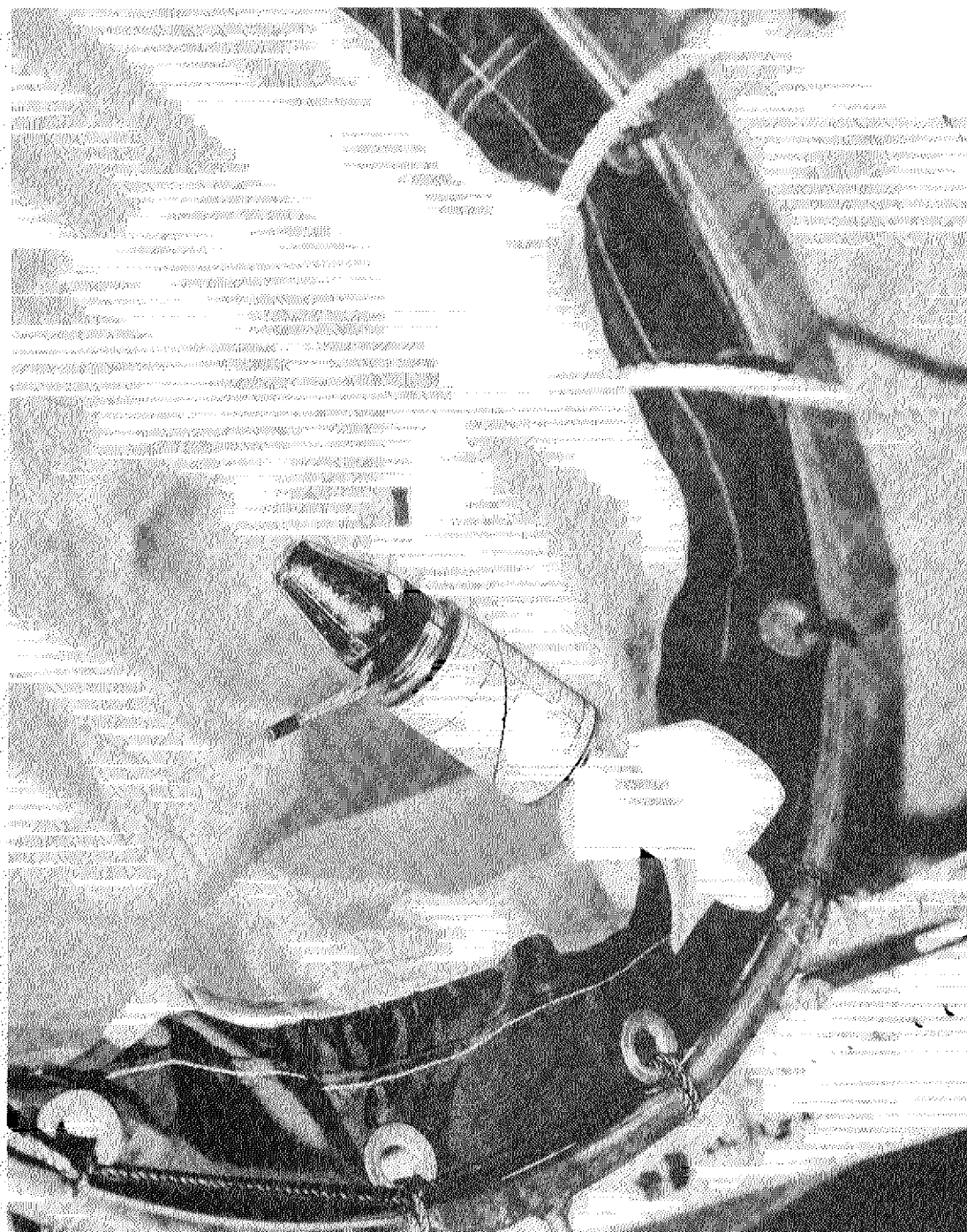
Appendix Figure 1. Port San Juan salmon hatchery and Sawmill Bay viewed from the air.



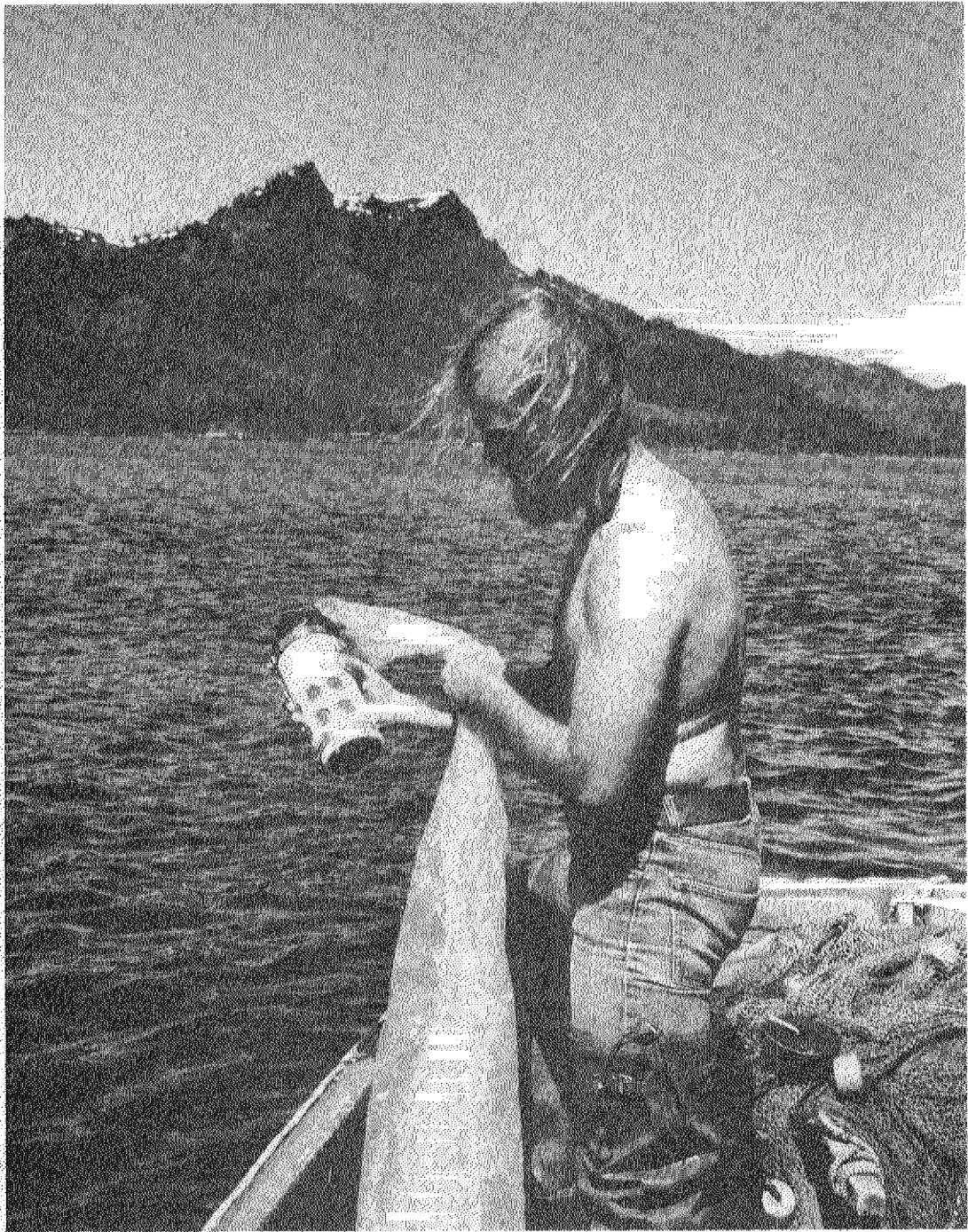
Appendix Figure 2. Floatplane delivery of mail, provisions, and passengers is a weekly occurrence.



Appendix Figure 3. Preparing a hydrographic cast for water samples.



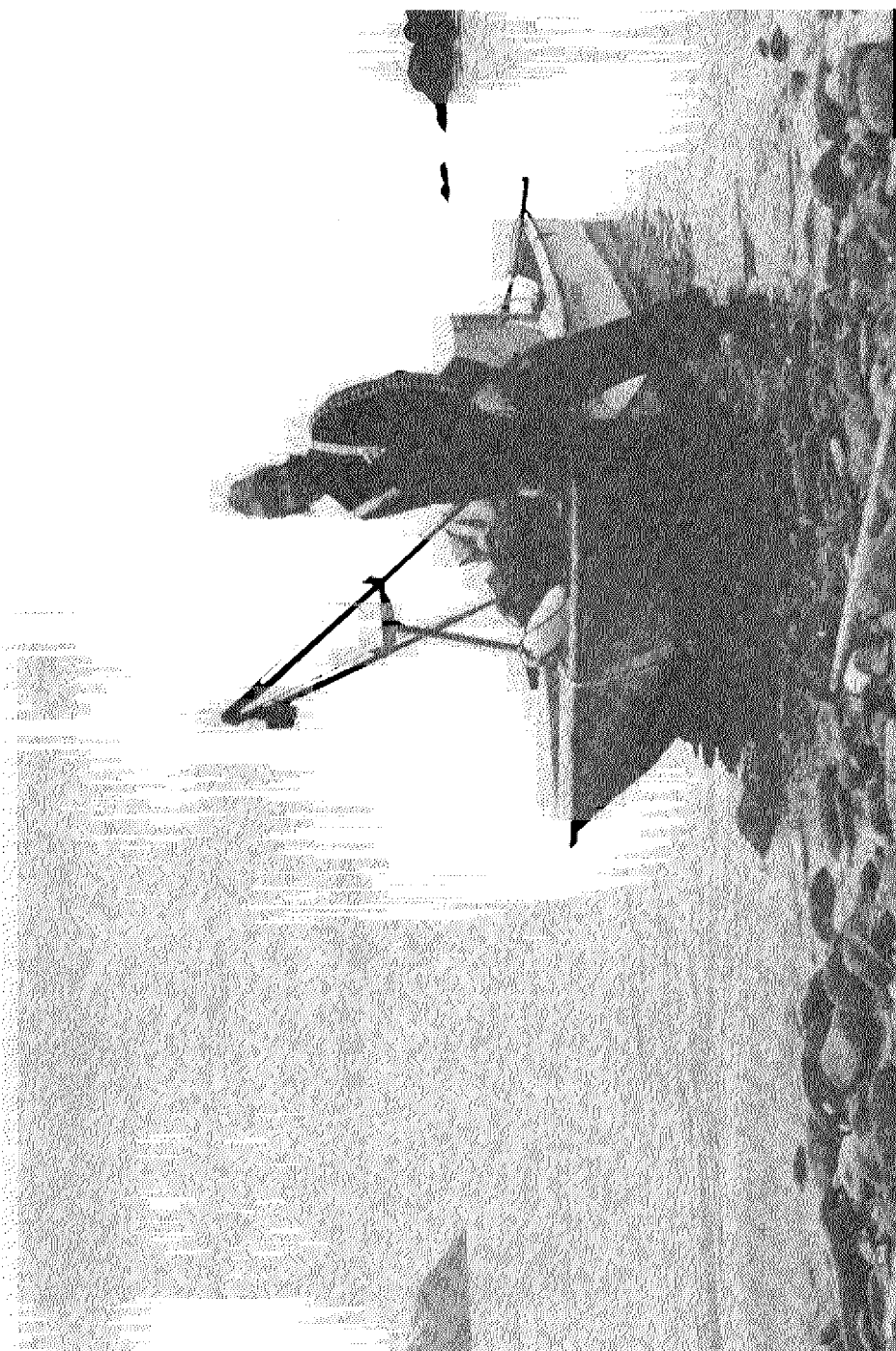
Appendix Figure 4. A one-half meter plankton net and flowmeter.



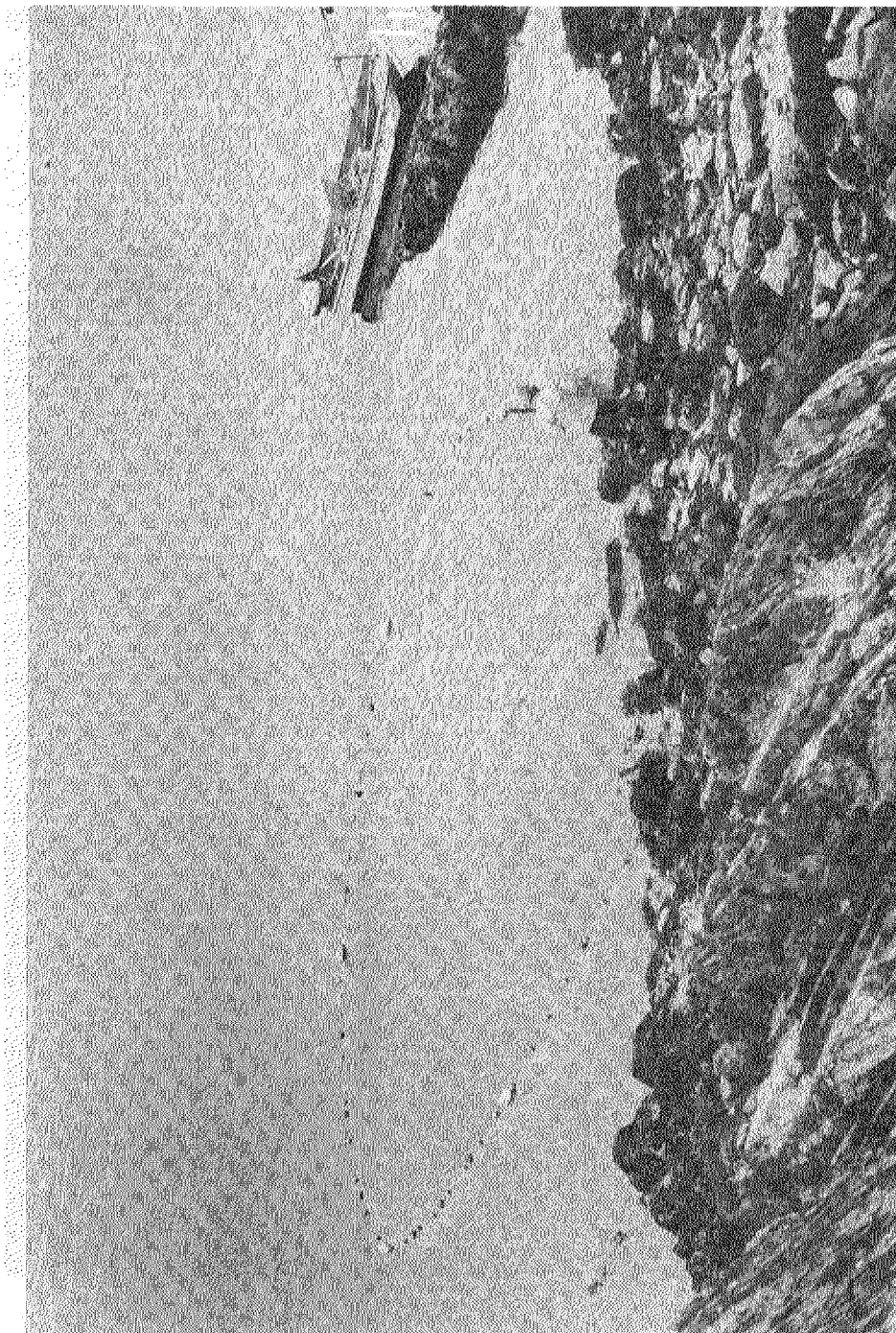
Appendix Figure 5. Preparing to preserve a zooplankton sample.



Appendix Figure 6. Examination of fry stomachs at the Port San Juan laboratory.



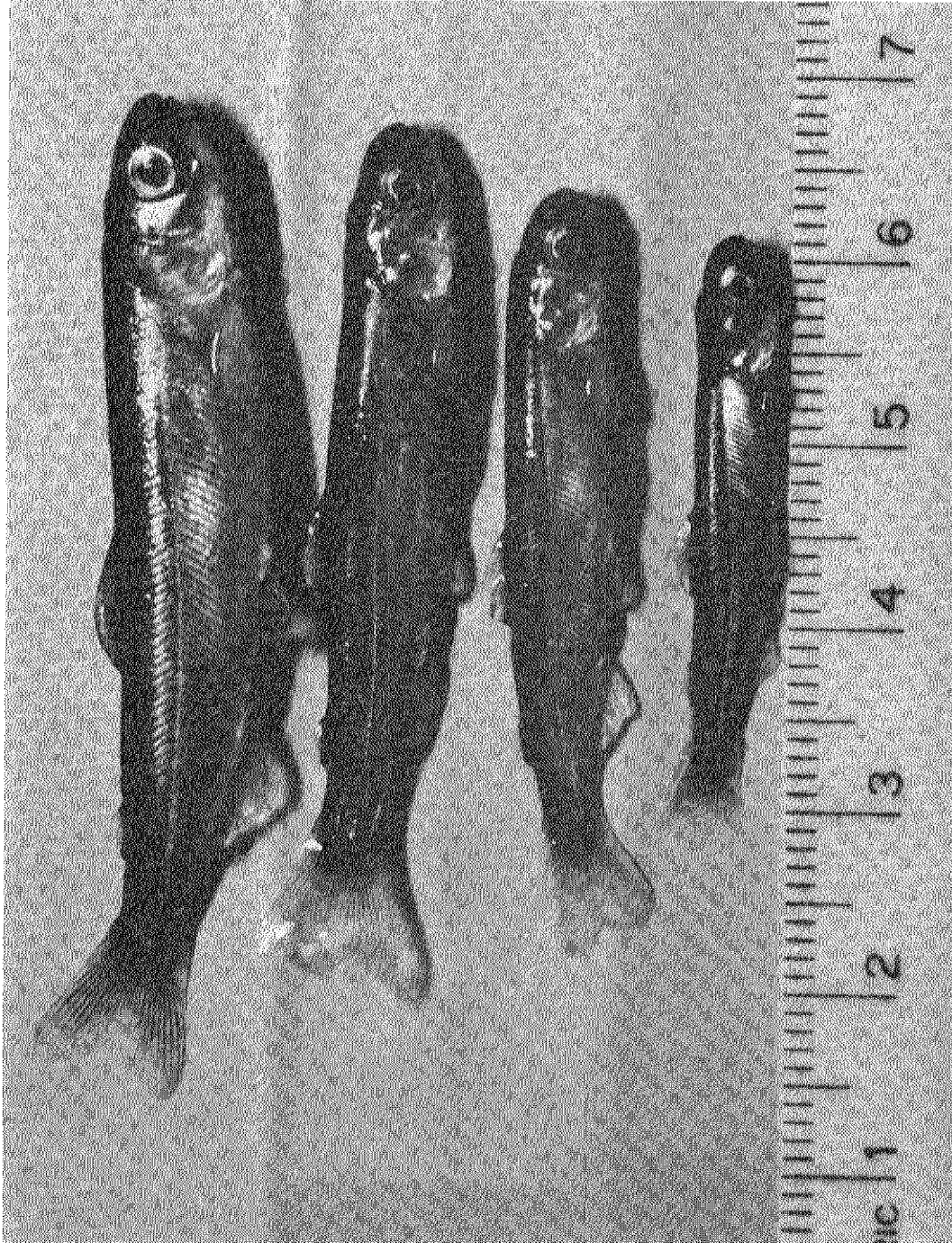
Appendix Figure 7. Getting ready to set the 100-ft beach seine.



Appendix Figure 8. The beach seine in position around a school of fry.



Appendix Figure 9. Examining the catch.



Appendix Figure 10. Preserved fry showing growth over the six week stay in the nursery areas. The smallest fish demonstrated the size at emergence from the hatchery.



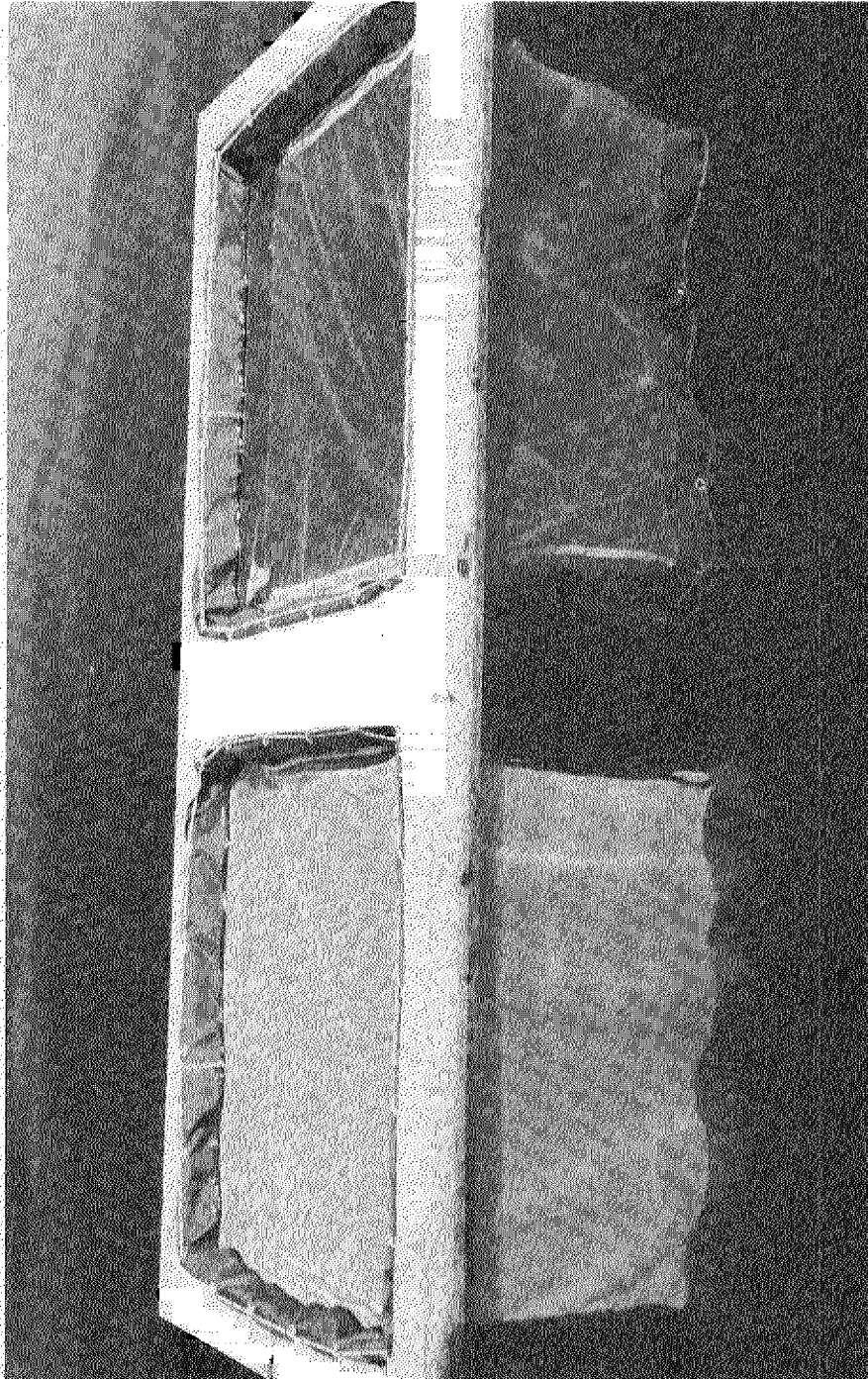
Appendix Figure 11. A sample of pink salmon fry taken late in the summer from a nursery area.



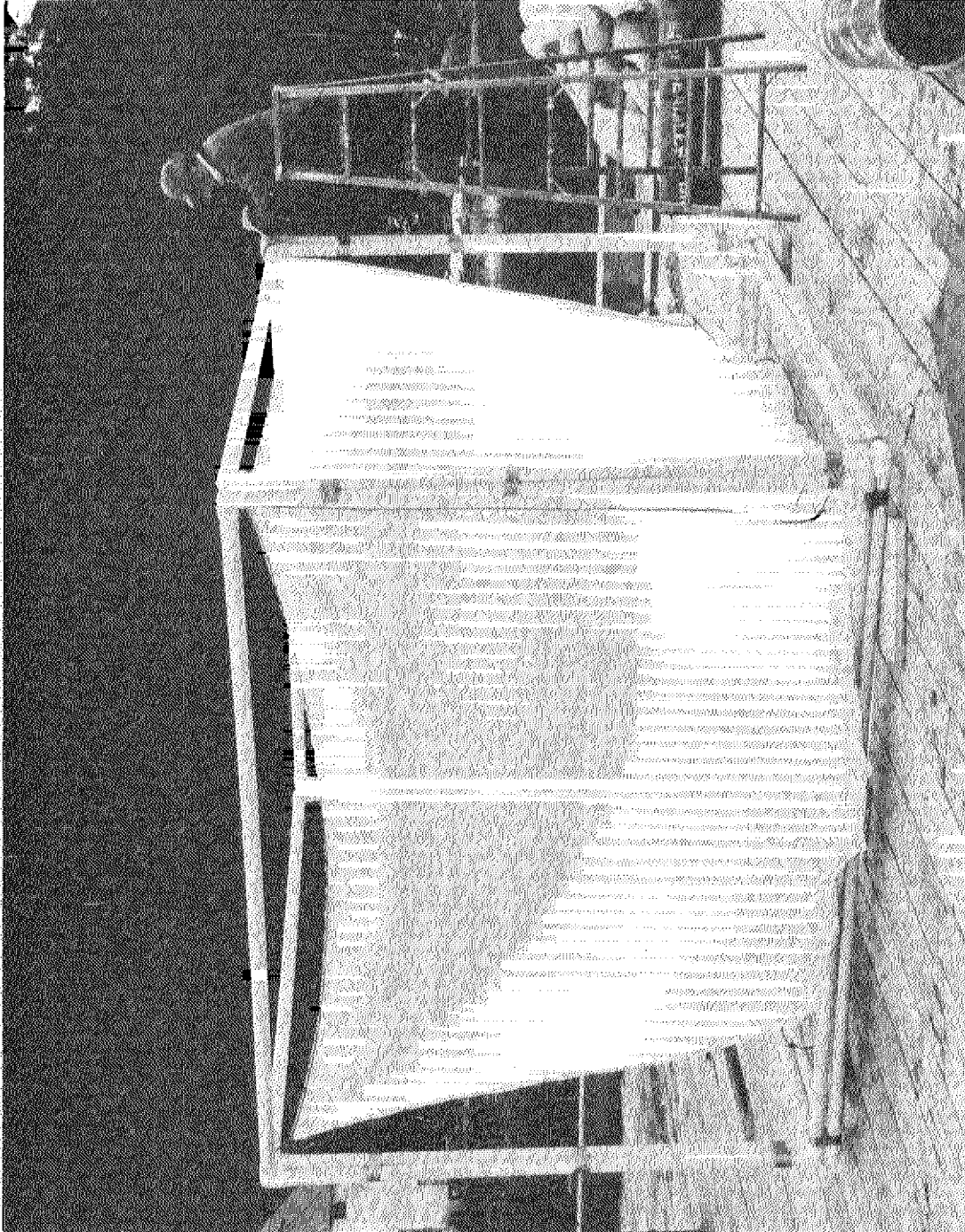
Appendix Figure 12. A small school of fry as seen in the nursery areas.



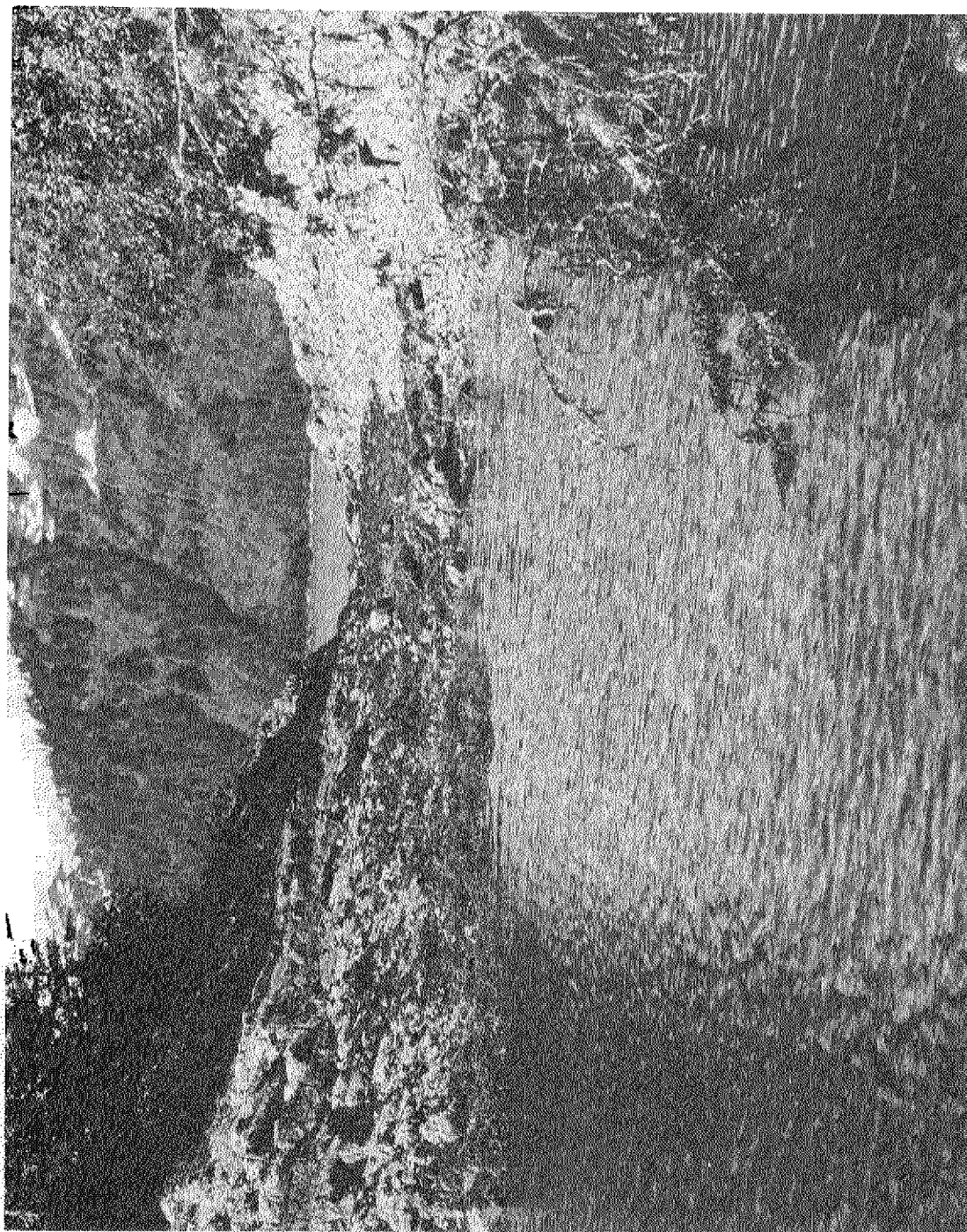
Appendix Figure 13. A closeup of schooling fry. Note the single herring swimming with the smaller salmon.



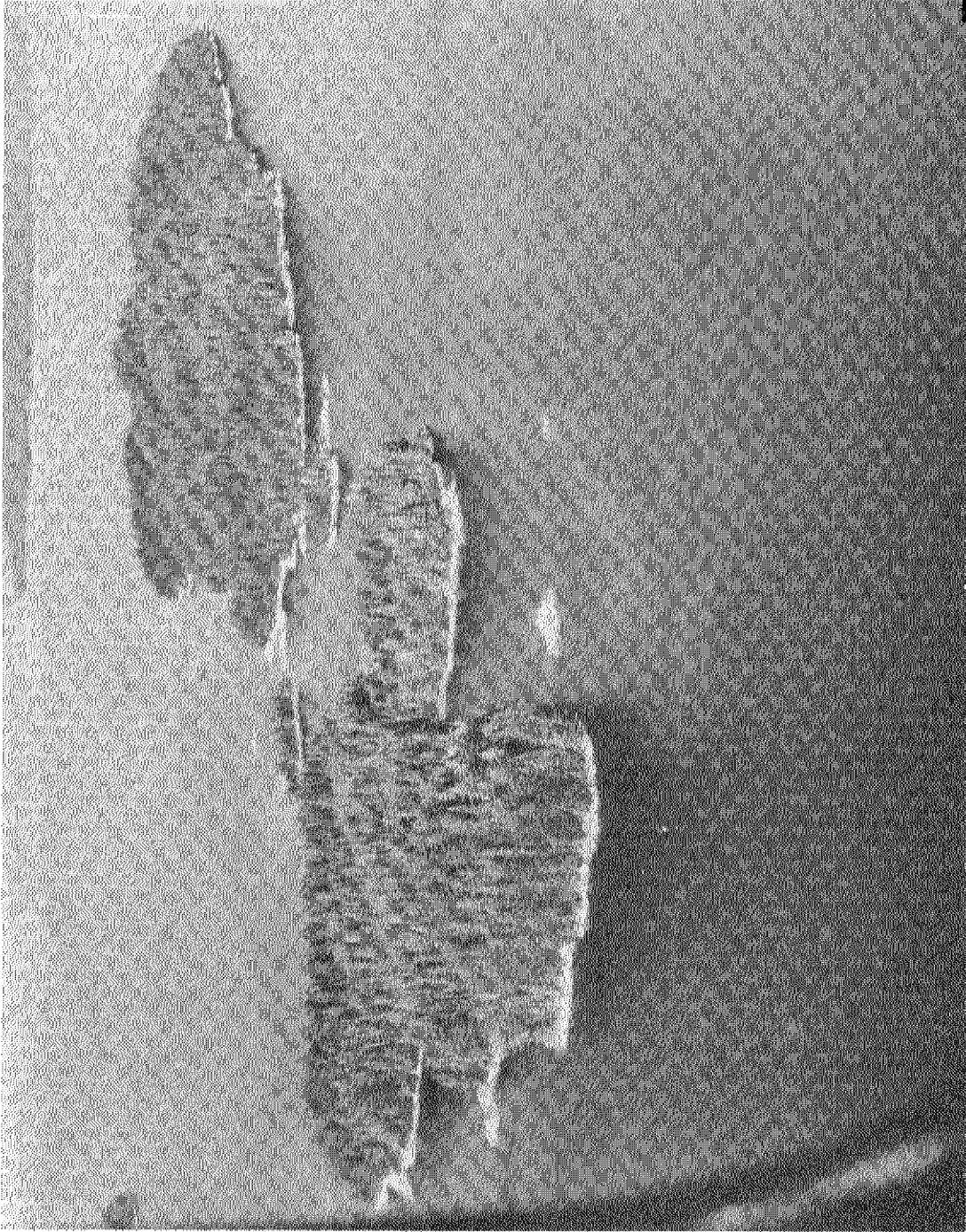
Appendix Figure 14. Experimental pens used for growth and starvation experiments; large mesh on the left, small mesh on the right.



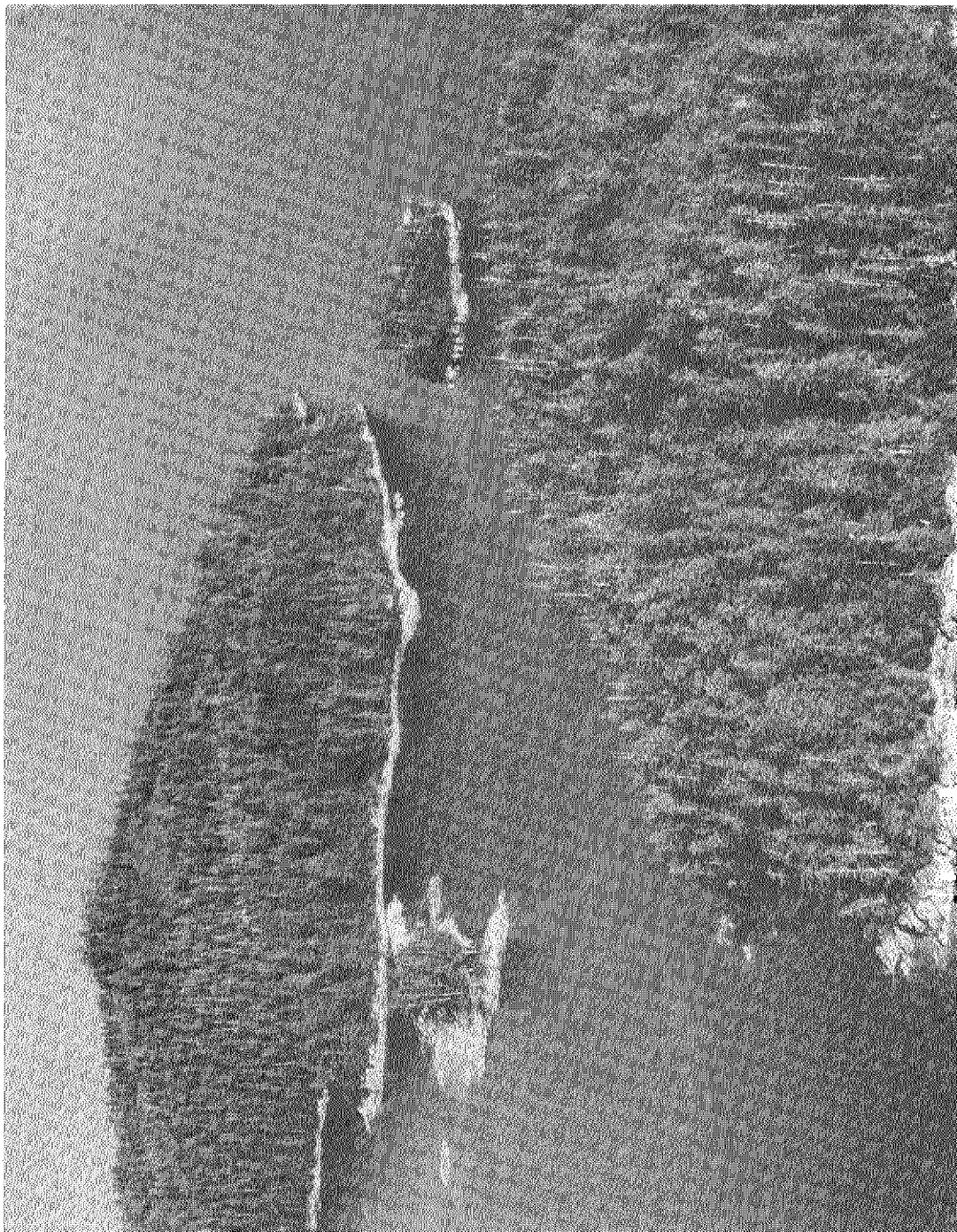
Appendix Figure 15. PWSAC holding pen being fabricated on the dock adjacent to the hatchery.



Appendix Figure 16. An example of a selected nursery in the foreground. Beyond the sill is Sawmill Bay.



Appendix Figure 17. A view of the island group supporting most of the nursery areas
(see Fig. 6 in text).



Appendix Figure 18. A closer view of the same islands. Site 0 is the small island to the extreme right in the center channel (see Fig. 6 in text).

APPENDIX II

A review of the early life history of the Pacific salmon prepared by David Urquhart as partial fulfillment of credit in W.F. 625, Fisheries Ecology offered fall semester by Dr. Willard Barber. The paper is appended because of its relevance to the overall study as presently undertaken and planned for the future.

FIVE SPECIES OF SALMON IN ALASKA:
A Discussion of Their Juvenile Ecology and Phylogenetic Relationships

by
D. L. Urquhart

Originally written for WF 625, Fisheries Ecology
Dr. W. E. Barber

INTRODUCTION

North Pacific waters are the home of the Pacific salmon (*Oncorhynchus* sp., Salmonidae). At present seven different species are included in the genus, six of which are anadromous. *O. rhodurus* is the landlocked species found in Japan's Lake Biwa (Vladykov, 1963). The cherry salmon (*O. masu*) spawns only along the western shores of the Pacific, principally in Japan where it is of commercial value even though of small size (Burner, 1964). The remaining five species: *O. kisutch*, *O. tshawytscha*, *O. nerka*, *O. keta*, and *O. gorbuscha* are commonly known as coho (silver), chinook (king), sockeye (red, blueback), chum (dog), and pink (humpback) salmon.

These five species occur throughout the North Pacific region from Japan through Siberia into the Bering and Chukchi Seas. Chums and pinks have been found as far west as the mouth of the Lena River and as far east as the McKenzie (Neave, 1958). The five species are indigenous to the west coast of North America from Alaska to southern California. Chinook salmon were most abundant in California being found in the Sacramento-San Joaquin River system and cohos were commonly found running in the smaller coastal streams of the state (Shapovalov and Taft, 1954).

All five species have the same general life history in Alaska. Adults migrate from the ocean to the freshwater streams from which they originated in order to spawn. This usually takes place in the fall, with the female depositing anywhere from 1,000 to 10,000 eggs in the gravel while the male simultaneously releases sperm. All species assume distinctive and conspicuous colors and shapes during spawning. The commitment of body resources to successful reproduction is total and in all instances results in death. Eggs incubate at varying rates in the fall

and early winter depending on water temperature (Neave, 1966). The eggs usually hatch after three months although they have been known to incubate five months or longer (Vladykov, 1963). The larval salmon (alevins) remain within the protective and supportive interstitial spaces of the stream gravel for many weeks after hatching. There they live off the reserves of yolky material so generously supplied by their parents until approximately April at which time they emerge to begin searching for food.

It is after emergence that the five species of salmon begin to diverge somewhat in their behavior and in the partitioning of environmental resources. The length of time the juvenile salmon spend in freshwater varies. Some go to sea immediately whereas some spend from one to four years living in streams and lakes. Eventually however, all migrate to sea. While at sea the pacific salmon acquire most of their growth and again varying amounts of time are spent there. Eventually the salmon, through some unknown mechanism, return to their home stream following their sojourn at sea, thus completing the cycle.

ORIGIN OF THE PACIFIC SALMON

Regardless of the reason for the branching of an ancestral group into several incipient lines, ecological and morphological divergence is usually the result. The point to be made with this rule insofar as the salmon are concerned is that the process has not gone very far. In some instances it is necessary to use features such as the number and length of the gill rakers, the number of scales, and the number of anal rays to distinguish between the species. Okada and Nishiyama (1970) found it difficult to distinguish between chum and pink salmon juveniles within an estuary using

these methods. As a result they made a study of additional morphological features that can be used to differentiate between the two species.

Neave (1958) feels that the physiological and ecological differences among the species of Pacific salmon appear to be even less sharp than the morphological distinctions. Preferred temperatures for all juveniles are 12° to 14°C and lethal temperatures according to Brett (1952) range from 23.8° to 25.1°C. Chum and pink salmon are frequently found breeding in the same locations at the same time and are known to produce viable hybrid offspring. Chum and pink fry are often found schooling and feeding together (Kaczynski *et al.*, 1973). Spawning and emergence of coho and chinook salmon are also known to overlap in time and space (Stein *et al.*, 1972). For species existing in sympatry, with little difference in behavior or general appearance, distinctive shapes and conspicuous coloration taken on during breeding are important in effecting and maintaining separation. As mentioned, this is the case in the genus *Oncorhynchus*. Sympatric situations are common for the five species of Pacific salmon found in North America (Hallock and Fry, 1967). Since breeding color patterns are apparently all that maintain species segregation and prevent merging, it is apparent that physical separation of the ancestral stocks must have occurred at some point. It must have been during this period of separation, or during these periods, that the existing species of *Oncorhynchus* developed their distinctive color patterns. Not surprisingly a geographical isolating mechanism has been invoked as the cause of this speciation. Since the evolutionary divergence has not gone far, this isolating barrier is thought to have developed during the Pleistocene epoch (Flint, 1947).

The Pacific salmon are believed to be of freshwater origin because of a universal habit for breeding and incubating eggs in freshwater. While there are several forms such as the kokanee (Foerster, 1968) which spend their whole life in freshwater, there are none that are entirely marine. *Oncorhynchus* probably stemmed from the genus *Salmo*. The sea-going rainbow trout or steelhead (*Salmo gairdneri*), because of its physiological capacity to handle salt, is high on the list as being the modern trout most closely related to ancestral *Oncorhynchus* (Hoar, 1976). According to Neave (1958) there was a "faunistic connection" between the Atlantic and Pacific across the Arctic in the late Pliocene. *Oncorhynchus* may have evolved as a result of *Salmo* reaching the North Pacific: "In one of the farthest regions to which it penetrated, a large stock became isolated geographically and diverged markedly from the populations which continued to inhabit other coastal regions of the North Pacific. In due course the newly evolved offshoot spread back through territories occupied by more conservative lines of ancestral stock. This process of reinvasion was facilitated by increased adaptation to ocean life and was accompanied or followed by further splitting up into several species" (Neave, 1958). Neave (1958) feels that the rise and fall of sea level brought about by the glacial periods of the Pleistocene could have caused the initial separations and later reintroductions.

The Sea of Japan is shallow and was probably cut off from the rest of the Pacific during periods of heavy glaciation. It was here that the geographically isolated ancestral salmon was able to develop its pelagic behaviors and abilities to tolerate brackish waters. Thousands of years later with the general warming of the planet and subsequent rise in sea level, *Oncorhynchus* was able to leave its birth place and reinvade the

Pacific. By this time enough evolutionary changes had occurred to permit continued divergence when contact was reestablished with the main stock of *Salmo*. Evidence to support this theory comes from the fact that both *O. masu* and *O. rhodurus* are somewhat more trout-like than the other five species. Furthermore both are today found only along the Asiatic coast (Hoar, 1976; Vladykov, 1963). *O. masu* is considered to be primitive because while anadromous, many mature in fresh water. When they do go to sea they do not range very far from shore. Cherry salmon are considered to be coastal in nature in comparison to the other anadromous salmon (Tanaka, 1963). A final point is that the land within the general vicinity of the Sea of Japan is the only area of the world at that latitude which does not support indigenous populations of *Salmo* (Neave, 1958). Trout have apparently not been able to reinvade the area since the establishment of the original population which became *Oncorhynchus*.

Subdivision of the ancestral *Oncorhynchus* stock into the seven species that exist today was probably brought about by further separations caused by subsequent glacial and interglacial changes in sea level. The Pleistocene epoch is thought to include four major glacial periods (Flint, 1947). The Sea of Japan is known to have been physically isolated from the Pacific Ocean three times during the late Pliocene and early Pleistocene (Neave, 1958). It is also thought that the great sheets of ice which developed in British Columbia during the Pleistocene ice ages could have effected further speciation. These glacial masses are known to have come right down to the coast, covering all the land between Oregon and the Aleutians. Any stocks of primitive salmon breeding in these areas would have been forced to move south, becoming isolated from the rest of the forms breeding elsewhere in the Pacific.

JUVENILE ECOLOGY

A good way to come to an understanding of the phylogenetic interrelationships among the salmon found in Alaska today is to examine patterns of juvenile behavior, physiology, and aspects of their ecology.

The main trend in speciation that has gone on within the genus *Oncorhynchus* has been the development of the ability to go to sea. The success of the genus seems to be based on the ability of the species to take advantage of the tremendous amount of food to be found in the pelagic zones of the North Pacific. Variations in the juvenile ecology of the five species stem from divergent paths taken in getting to sea. Some go to sea earlier than others and it may be that natural selection has progressed along lines that favor the development of this ability at an earlier age in the life of the individual fishes. By examining various aspects of juvenile ecology we can expect to come to some conclusions as to which species of the five being considered is the most primitive and which is the most advanced. It will also be possible to rank the salmon into an order where the abilities in this regard are somewhat intermediate.

The two areas of juvenile salmon behavior and physiology that most reflect the varying ability to go to sea are (1) the ability to osmoregulate and (2) variations in behavior patterns relating to migrations that carry the fish to sea.

OSMOREGULATION

One of the most interesting changes that takes place in the life of a salmonid is the development of the ability to osmoregulate. According to Hoar (1976) non-migrating salmonids show a sharp increase in salinity

resistance during spring. Its magnitude is size dependent and is brought about by the lengthening of the day and an increase in water temperatures. The ability is independent of a smolt transformation and subsides if the fish is retained in freshwater part of the time of migration. Salmon fry have elaborated upon the ability trout have developed for osmoregulation and today exhibit three basic responses. The ability may (1) appear prior to the parr smolt transformation, (2) develop gradually over the whole period of juvenile existence, or (3) always exist (Parry, 1960).

Coho and Sockeye

Coho and sockeye salmon are adaptively anadronous. Most go to sea although both are capable of completing their life cycle in freshwater (Foerster, 1968; Dvinin, 1960). When they do go to sea, like some species of *Salmo* (*S. gairdneri*, *S. salar*, *S. trutta*), coho and sockeye parr experience a strong smolt transformation (Parry, 1960) with marked changes in appearance and behavior. It is not however a reversible process as it is for *Salmo*.

Coho and sockeye parr are colorful fish that blend in well with their background. During the smolt transformation this coloration is lost and replaced by the silvery sheen of a pelagic fish, the adaptive significance of which is obvious. Deposition of purine layers in the skin account for the change in pigment. The transformation involves a number of complex physiological changes including a fall in body fat content, and an increased rate of growth (Hoar, 1976). The smolt is a trimmer and more streamlined fish than the freshwater parr.

Smolting in coho and sockeye is associated with a change in water preference. Smolts prefer seawater (McInerney, 1964) although the ability to osmoregulate also appears to be independent of the transformation. Coho are able to withstand full strength seawater a few months before they begin to migrate (Wagner *et al.*, 1969). The ability to successfully osmoregulate is related to the size and age of the fish (Parry, 1960). Prior to smolting, coho and sockeye prefer water in which salinity never goes beyond 3 percent Cl (McInerney, 1964). As fry they will experience lethal elevations in serum ion concentrations if exposed to full strength seawater (Weisbart, 1968). It takes coho and sockeye juveniles many months or years of growth to develop to the point where they become resistant to a hyper-osmotic environment.

Coho will spend anywhere from one to four years in fresh water before smolting and going to sea for a non-variable 12 to 18 months (Crone and Bond, 1976). Sockeye spend one to five years in fresh water before smolting and one to three years at sea (Groot, 1965; Hartman, 1971). Time spent in fresh water is dependent on temperature and therefore, to some extent on latitude. In California the average coho spends one year in freshwater (3(2)) (Shapavalov and Taft, 1954) whereas in Alaska according to Drucker (1972) the average is two years in fresh water (4(3)). It takes longer to grow in colder northern waters to the size needed for successful osmoregulation in seawater. Coho smolts are 100 to 150 mm in length after one to three years spent in Alaskan streams (Drucker, 1972). Sockeye smolts are from 80 to 140 mm in length after one to three years spent in a British Columbian Lake (Foerster, 1968).

Chinook

The chinook is obligated to go to sea to complete its cycle. Also cryptically colored while in freshwater it does not experience a precise and sudden smolt transformation. Along the coast of North America several races of chinook salmon are generally recognized and named with the season during which the adults return to freshwater (fall, winter, spring) (Mason, 1965). Alaska supports primarily spring chinook which enter freshwater in May or June and complete spawning by August (personal communication with ADF&G). The extent of time the fry spend in Alaskan freshwater is generally confused by the tremendous distances the fish sometimes have to travel to reach the sea. In southern California chinook fry are forced to go to sea a few months after hatching in order to avoid lethal summer river water temperatures (Hallock and Fry, 1967). In Alaska's Yukon River it may take one or more years for the fry, which emerge in the spring, to reach the sea. This is speculation. Chinook too, mature at a greater age the farther north they occur. In southeast Alaska the principal ages are three, four, and five. Ages range from five to seven years in the Yukon River and four to six in Cook Inlet (Yancey and Thorsteinson, 1963).

Chinook salmon hatch with a greater ability to resist a hyperosmotic condition than coho or sockeye. Chinook alevins can tolerate a salinity of 15 ppt for extended periods (Wagner *et al.*, 1969). As with coho and sockeye fry, emergent chinook fry are stenohaline and unable to regulate the ion content of their blood serum. However they exhibit a higher tissue tolerance and are therefore able to reside in more brackish water than coho and sockeye of the same age (Weisbart, 1968). Although chinook succumb to full strength seawater as newly emergent fry, it takes them much longer to die than coho or sockeye. The chinook, unlike the coho

and sockeye, acquires the ability to osmoregulate gradually while in fresh water without any sharp increase associated with a smolt transformation (Hoar, 1976). Within four months chinook are able to go to sea; this usually takes place within the first 16 months of life (Wagner *et al.*, 1969).

Chinook are well prepared for a fairly rapid transfer into brackish and estuarine waters. Early exposure to salts results in acclimation and stable maturation of the regulatory mechanism at an earlier age. This ability may have developed as a means of avoiding competitive interaction with coho. Juvenile coho and chinook are both territorial while in streams and are often found in sympatric situations. Stein *et al.* (1972) has shown however, that the chinook are unable to succeed and grow in the presence of the more aggressive coho. The situation is only relieved when within two to three months the chinook begin to migrate down-stream either into the estuary or deeper, faster parts of the river, leaving the coho to the shallow upstream areas (Stein *et al.*, 1972; Reimers, 1968). The chinooks' ability to tolerate high salinity certainly has much to do with successful partitioning of the environment by these two recently divergent species.

Pinks and Chums

Pink and chum fry are euryhaline and although the alevins of all five species are considered to be stenohaline, the pink, and chum alevins have greater osmoregulatory abilities than the others (Weisbart, 1968). Pink and chum fry experience a rise in serum chlorides during the first 6 to 8 hrs they are exposed to seawater after which they actively regulate their serum ion levels. They are characterized by suppression of the smolt stage (Hoar, 1976) and are ready to go to sea upon emergence. Chum fry are cryptically colored to an extent. The pink begins its life as a silvery pelagic animal (Horar, 1958).

The pink salmon fry migrates immediately upon emerging from the gravel (Healy, 1967; McDonald, 1960) taking no food until established within an estuary. The amount of time a pink salmon fry spends in fresh water is dependent only on the speed at which it can swim and the distance it must travel to reach salt water. Once established within an estuary the pink remains there several months before going to sea. The pink is on a strict two-year cycle with only few instances recorded of adults being older (Anas, 1959; Turner and Bilton, 1968).

Chum are also capable of moving straight into salt water and are generally thought to do so. Mason (1974) however, reports that such is not always the case. Chum exceeding 80 mm in length have been found in streams a short distance from the sea where they were actively feeding on stream drift. Mason (1974) observed chum going through daily cycles where they would actively move from fresh water streams into an estuary and then back again several times a day. They appeared to be constantly moving against the tidal currents and were taking advantage of food organisms from both environments. Chums have life cycles lasting two to four years (Merrell, 1970). They are known to migrate up large rivers great distances to spawn, unlike the pinks which generally use small coastal streams. As mentioned, chum salmon are also often found in association with pinks, both as adults during spawning and as fry in mixed schools near shore on the surface (Bailey *et al.*, 1975; Okada and Nishiyama, 1970; Kaczynski *et al.*, 1973).

JUVENILE SALMON MIGRATORY BEHAVIOR

Juvenile salmon will be discussed below in terms of behaviors and characteristics that will lend insight into their preparedness to go to sea at an early age. Hiding, schooling, feeding, predator avoidance, and territory occupation are behaviors among those that will be discussed. Variations of the manner in which the fish accomplish these tasks account for many of the differences in migratory behavior. Much of this material is taken from W. S. Hoar (1958). Information from other sources will be referenced in the usual fashion.

Coho

Coho salmon tend to spawn close to the coast in short streams with steep gradients and fast running water. They are also found in tributaries of some of the larger rivers (Godfrey, 1965). Fry are 32 to 34 mm in length when they first emerge from the gravel, intermediate in size with respect to the other four species. They are yellow brown with dark brown backs. Parr marks are dark, narrow, and extend well past the lateral line. Fins are large and orange, tinged with white on the leading edges (Stein *et al.*, 1972).

The coho, unlike the pink, chum, and sockeye, shows no preference for emerging from streambed gravel during the night (Mason, 1975). It is, however, as are all five species, initially photonegative and it tends to hide and stay in the shadows. This photonegative response soon wears off for the coho and changes to photopositive behavior. Coho acclimate to repeated disturbances. They become quite used to changing light patterns and flickering shadows, a necessary adaptation for a fish geared to life in a shallow stream (Hoar *et al.*, 1957). Active during the day, coho

fry will settle to the bottom at night and cease to swim or feed. This prevents inadvertant downstream migration through the loss of orienting visual contact with the surroundings. For pink and chum fry downstream migration is nocturnal and appears to arise from displacement by the current when visual contact is lost with fixed objects in the stream (McDonald, 1960).

The coho that first emerge from a redd show a strong tendency to move into upcurrent sections of the stream (Mason, 1975; Crone and Bond, 1976). In many cases this puts these fish at an ecological advantage in terms of position for stream drift and relative food abundance. The fry first to emerge will outstrip in growth the fry emerging later and be able to maintain advantageous positions in the stream through size dependent dominance. Seeding also enables fry to utilize shallow stream sections where adults were unable to spawn, thus increasing the streams overall productivity.

Within ten days of emergence coho become extremely aggressive and attempt to establish a well defined "territory" within the stream. It is within this territory that the young coho maintains position in the water column, feeding on drift, rising to the surface to take floating food particles. Other coho and species are repelled by dominance posturing, redirected aggression, lateral display, chasing, rapid circling, and severe nipping at the caudal region (Mason and Chapman, 1965). Coho always over-spawn. Those fry which are unable to secure a territory are forced downstream and if into an estuary, it is unlikely they survive to reach adjacent streams (Mason, 1975). These behaviors very definitely limit the number of individuals a stream can support and probably account

for the fact that coho are not an abundant salmon in relative terms (Godfrey, 1965).

The territorial system set up by a population of coho is not without flux and shifting of territories. Older fish which are piscivorous and cannibalistic, smolt and make room in the stream for the newer year classes. Coho also move into deeper pools and riffles as they grow. Aggression is usually higher in groups of coho equivalent in size. It is higher in the evening with an increase in the oviposition of adult aquatic insects on the surface. Once territories for a new year class have become established fighting settles down. By the time coho reach 45 to 48 mm in length aggressive displays are rare (Mason and Chapman, 1965).

Coho juveniles form schools when they are badly frightened. When scared by an overflight of birds or some predator the coho flees its territory and seeks the deep pools of the stream. There the fish form close and temporary associations known as "fright huddles" (Mason and Chapman, 1965). During this period the fish exhibit rapid respiration, fin contact with the sediment and each other, and no aggression. During break up the dimension of the huddle slowly expands until an appreciable number of fish venture from it and return to their territories.

Coho do show "follow the leader" behaviors when placed in among a school of pink or chum fry. If adequate space is available however, the coho will soon settle out and continue their solitary existence. Coho do show schooling and migratory behavior in streams where the water flow is drastically slowed as it would be during a drought. Coho smolts do not school while in fresh water.

All coho spend at least one winter in fresh water. Overwinter survival is placed between 30 and 40 percent by Bustard and Narver (1975).

The coho do feed but at very low rates and they tend to seek cover more as temperatures drop. River banks and overhangs are important overwintering areas.

Smolting occurs in the spring mainly between April and June with a peak in May. During smolting a change in the photoresponse develops; coho smolts migrate to sea under the cover of dark (Mason, 1975). Coho smolts are often observed to feed on displaced coho fry moving out of the stream at the same time. Coho smolts are well-known for their predation on pink and chum salmon fry migrating to sea at the same time, along the same route (Parker, 1971).

Chinook

Chinook juvenile salmon behave in a manner similar to that of the coho. They are the largest of the emergent fry reaching lengths of 39 mm (Wagner *et al.*, 1969). They are silvery or light yellow with blue-green or brown backs. Parr marks are wide, black, and contrast sharply. Their fins are yellow and less conspicuous than those of the coho (Stein *et al.*, 1972).

Chinook are the only other territorial species of the five being considered. They tolerate higher densities of individuals on the stream beds than do coho. The extensive development of aggressive behavior and territoriality by the coho may be related to the extended periods of time they spend in the stream. Coho must adjust their population levels to periods when space, due to water flow, and food are reduced (Stein *et al.*, 1972). Chinook are not constrained in this way because they are prepared to go to sea or begin their migration by the end of their first summer. In those streams where both species spawn the chinook will

occasionally emerge from the redds first. This enables the chinook to outgrow the more aggressive coho, minimizing interaction, and prevents the chinook from being run out of the stream (Lister and Genoe, 1970).

It is not known whether the indifferent behavior chinook do display results in the dispersal downstream of the smaller fry. Differences in the length of stay in freshwater by members of the same age class have been noted (Reimers, 1968). After three months in the shallow upstream environment, chinook move into the deeper waters of the main river or estuary (Stein *et al.*, 1972).

Chinook form "fright huddles" under the same conditions as the coho. Schooling has been observed among groups of chinook in large pools of freshwater and in estuaries. It is assumed that orientation and maintenance of position are impossible under these conditions (Reimers, 1968). Members of the school move freely within it feeding on the surface. When visual contact with the bottom is reestablished close to shore milling and breakup of the schools tends to occur. The schools are observed during the day. No light avoidance has been observed among schooling chinook. Chinook lose the tendency to avoid light after a few days spent in the stream.

Chinook feed on drift in the streams by lying close to fast water areas. As with the coho they occupy much the same microhabitat the steelhead occupies. Insects make up the bulk of the diet (Everest and Chapman, 1972). Once within the estuary, Kask and Parker (1972) found amphipods, isopods, and larval aquatic insects to be important nearshore. Offshore in the estuary they fed on mud-dwelling cumaceans, copepods, cladocerans, fish larvae, euphausiids, decapods, chaetognaths, barnacle larvae, polychaetes, and cephalopods. Kask and Parker (1972) felt this

variety of organisms suggested chinook juveniles were not restricted to feeding at a particular depth.

Sockeye

Sockeye emerge as the smallest of the salmon fry being considered, being 25 to 29 mm in length (Hartman, 1971). They have a definite row of black spots on a bluish or greenish back. Their elliptical parr marks do not extend much below the lateral line into a lightly colored lateral and ventral surface (Foerster, 1968).

Sockeye emerge at night from the gravel of streams which are inlets or outlets of lakes. Some sockeye spawn in the lakes themselves at depths to 100 ft (Groot, 1965). They are the most photonegative of the juvenile salmon (Hoar *et al.*, 1957). Initially the sockeye hide during the day near the bottom. Within a few weeks the sockeye become more active under illumination but they never show the strong light preference of the other species (Hoar *et al.*, 1957). The fry migrate to the lake singly feeding on drift along the way. Because they are so small it often takes them some period of weeks to make their way to the lake. Migrations take place during the darker hours (McDonald, 1960). At the slightest disturbance or increase in illumination migrating sockeye fry will dive to the bottom of the stream and hide. They do not become acclimated to repeated disturbance. While in the streams they show some tendencies toward territoriality and will occasionally chase one another although without nipping. This activity is more strongly developed in sockeye smolts.

Sockeye fry enter the lake in which they will spend the next few years just prior to the onset of the plankton bloom (Foerster, 1968).

There they school up foraging along the shore for a short period before moving into the deeper open water areas of the lake (Groot, 1965). The schools formed by the sockeye are stationary planktonic aggregates of fish with little directed motion. The sockeye show random orientation within a school. This is in contrast to constantly moving polarized schools formed by pink and chum salmon within an estuary. The sockeye schools do not move over the entire lake. Rather, according to Groot (1965), the fish tend to remain localized in areas close to their respective spawning streams. A single lake may thus support several distinct populations of sockeye.

While within the littoral zone of the lake the sockeye, now called fingerlings, feed on crustaceans, insect larvae, and terrestrial insects that fall on the surface. When they move to the deeper areas the diet changes and they feed on planktonic crustaceans: copepods (*Cyclops*, *Diaptomus*, *Heterocope*), cladocerans (*Daphnia*, *Bosmina*) (Foerster, 1968). Sockeye fingerlings are known to undergo diel vertical movements within the lake especially when the water is stratified during the warmer months. The fingerlings may be following the planktonic community as it undergoes diel vertical movements. The schools rise to the surface at dusk and break up as individual fish scatter across it to feed. The fry settle to about 10 m to pass the night, rising again at dawn to feed. The day is passed below the thermocline at depths of 35 to 55 m (Foerster, 1968). During these warm months the fingerlings eat upwards of 70 percent of their body weight/day. Although hymenoptera, diptera, and chironomids alighting on the surface contribute to their fare in the summer, *Cyclops* are the year round mainstay. Individual sockeye fingerlings exhibit feeding preferences.

Migrations out of the lake occur first for the larger smolts of each year class. This takes place shortly after the ice melts and lasts many weeks. The smolt transformation is associated with an increase in sockeye's already pronounced photonegative behavior. The smolts migrate downstream to sea in spurts during dusk and again at dawn (Groot, 1965). The smolts school as they move downstream swimming actively, seemingly led by the larger individuals (Foerster, 1968). In areas of higher currents the smolts tarry and then move downstream tail first.

Once within the estuary the sockeye remain about two months before proceeding offshore. They tend to stay on the surface following the shore. The sockeye feed on planktonic copepods and larvaceans much as do the pinks although small fish are also important (herring larvae, and sand lance) (Manzer, 1969). Once at sea they are generally considered to be the most planktophagous of the salmon although squid, shrimp, and small fish are also important (Hartman, 1971). They are the most desirable of the salmon commercially because of the rich red color of their flesh and its high oil content.

Chum

Chum fry emerge from the gravel 34 to 36 mm in length. Only chinook fry are bigger. They have greenish backs, being silver on the sides and belly. Dark parr marks extend to the lateral line. These fade rapidly once the fish enters the estuary. The chum emerge from the gravel at night and may either go straight to sea or spend several weeks in the stream (Mason, 1974). Within the stream the chum act as individuals feeding on drift. Some aggressive chasing after other individuals and species from preferred feeding stations has been observed. They are however, not

generally considered to be territorial. Within the estuary chums form schools very much like those of the pink, although when in shallow calm areas the schools tend to be diffuse.

Once chums have emerged they show a preference for bright areas that exceeds that of schooling pinks (Hoar *et al.*, 1957). They show little tendency to hide from light even as individuals which have not yet schooled. Only under extremely bright light will a chum tend to retreat into shaded or deeper water. Unlike the coho, chum fry do not adapt well to repeated disturbance. Sudden changes in light intensity and surface patterns of illumination will elicit a diving response everytime.

Chum fry will dive to the bottom and hide among rocks while in a stream to avoid predators. They will also dive while in the estuary. Adult chum are notorious among fishermen for their ability to avoid nets by diving deep when startled. They are generally credited with a higher intelligence because of their ability to avoid capture.

Juvenile chum salmon are known for their tendency to feed on epibenthic organisms while in the estuary (Feller and Kaczynski, 1975; Kaczynski *et al.*, 1973; Brown and Sibert, 1977). Harpacticoid copepods seem to be the most important component of this diet and are selected on the basis of size (Feller and Kaczynski, 1975). It is assumed that juvenile chum take these organisms off the bottom. This is one point that needs to be investigated. The author feels it is quite likely the harpacticoids are taken on the surface. Chums are also known to feed on pelagic copepods and larvaceans (Bailey *et al.*, 1975; Manzer, 1969) during the first few months spent in coastal waters.

As mentioned, Mason (1974) reported observing schools of juvenile chum switching back and forth between fresh and salt water. Stomach analysis showed layers of freshwater gammarid amphipods to be alternating with layers of saltwater calanoid copepods. Apparently schooling chum would move against ebb tide until the mouth of a stream was reached. The school would then break up and the chum would take up stations in the stream and collect amphipods and insects. They were observed to chase off coho feeding in the same area and would head to sea again when the mouth was inundated by the flood tide. The coho, of course, would head upstream at this time to avoid the salt water. Juvenile chums are well adapted for coping with both a freshwater stream environment and a saline estuarine environment during the first few months of their free swimming existence.

Pink

Pink salmon emerge during the night from their redd ready to go to sea at 30 to 32 mm in length. Only the sockeye are smaller. They possess green backs, silver sides and belly with no parr marks (Bailey, 1969). They begin downstream migration immediately upon emerging, primarily through passive transport. They migrate singly and often reach the estuary within one night. They are photonegative and hide in the stream during the day if they are unable to reach the estuary the first night. Once within the estuary pink fry immediately form schools and lose their light avoidance behaviors. Experiments by W. S. Hoar (1958) have shown that once a pink fry experiences schooling, it will no longer avoid light, even if the experience lasts only a few minutes. Once the school is

formed the pinks will stay on the surface, 24 hours a day, in all but the brightest of lights (Hoar *et al.*, 1957; Healey, 1967).

Juvenile pink salmon show no aggressive behavior and no territoriality whatsoever. They are very poorly adapted to an extended stay in fresh water because they are not cryptically colored and will not dive to escape predators. Rather, they will scatter across the surface, at least for the first 40 days of free existence. Experiments run by W. S. Hoar (1958) showed pinks to have very low relative survival rates in streams for these reasons. When kept in fresh water pools that were frequently visited by predatory crows (*Corvus*), the pink fry were rapidly reduced in number. Other species of juvenile salmon kept in the same pools at the same time were able to avoid capture by diving and hiding.

Schooling juvenile pinks within the estuary stay generally in protected areas close to shore. They often form tight swirls of fish that move continuously. The fish feed from these schools principally on pelagic zooplankton (Bailey, 1969; Manzer, 1969) but to some extent on epibenthic prey (Kaczynski *et al.*, 1973). Calanoid copepods are the most important component of their diet.

After the first month spent in the estuary close to shore the schools tend to disperse somewhat and move offshore. The young pinks, by now 50 to 70 mm in length, tend to localize in areas swept by currents while they continue to feed on zooplankton. By the end of the summer the pinks have moved out to sea. Pinks are the "bread and butter" fish of the salmon industry. Their abundance is due to the fact that they are small and able to spawn in numerous small coastal streams that are too shallow for the larger species. They are also not limited in their abundance by

available nursery space. Since they are not territorial the number of fry that can be successfully reared by the environment is determined by the carrying capacity of the local estuary rather than by the size of the stream in which they were spawned.

SUMMARY

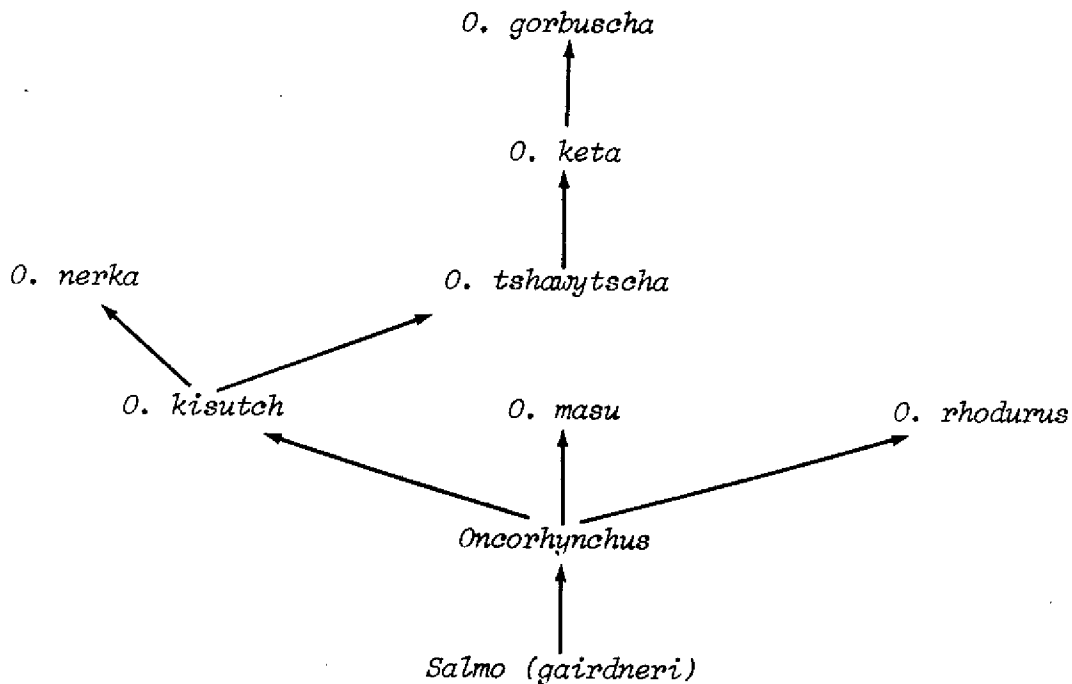
The speculation based on the above considerations is that for *Oncorhynchus* there has been an evolution in terms of an earlier internal motivation to go to sea. The main trend has been the development, at an increasingly early age, of an osmotic regulatory mechanism and a correspondingly early migratory behavior. The climax of this trend is seen in the pink salmon while the coho is considered to be closest to the parent type (Hoar, 1958, 1976; Neave, 1958).

In relating the other three species those abilities in this regard are intermediate, chinook and sockeye present something of a difficulty. Chinook are very similar to coho in everything except their osmoregulatory abilities. They go to sea quite early. The sockeye seems to have been sidetracked in terms of attempts to take advantage of the growth potential available for a fish going to sea at an early age. They are pelagic fish, though taking advantage instead of the lacustrine zooplankton community. Morphological and serological studies (Hikita, 1962 taken from Hoar, 1976) attempt to resolve the uncertainty by placing *kisutch* and *tshawytscha* on one stem, *nerka*, *keta* and *gorbuscha* on the other. Purely on the basis of osmoregulatory abilities, chinook should be considered to be intermediate and perhaps the parent type for chum and pink.

The chum, of course, possess behaviors and characteristics similar to those of the stream-dwelling coho and the ocean-going pink. Its

osmoregulatory abilities, coloration, and tendency to go to sea early however leave no doubt that it is closely related to the pink and should be considered a more modern form.

The following diagram of a phylogenetic tree is presented as one logical way of viewing the interrelationships among the salmon being discussed, based on the information presented in this paper:



The present situation can be seen as a continuing trend in the process of speciation for *Oncorhynchus* and should be considered to be quite transitory. *Gorbuscha* because of its strict two year cycle is really composed of two completely separate races that may logically be considered to be non-interbreeding subspecies. Similar arguments may be applied to the separate races of chinook salmon. The tendency salmon have to return to a home stream promotes the establishment of genetically

isolated populations. Since the end of the last ice age, for our five closely related species, allopatry has gone to sympatry. Interspecific competition results in either elimination of a species or the development of differentiating isolating mechanisms and divergence. For *Oncorhynchus* evolution continues at a rapid pace. It may be significant that the most abundant Pacific salmon is also the most specialized in terms of its breeding characteristics and its ability to go to sea at an early age.

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